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Crop Responses to Elevated Carbon Dioxide and Interaction with Temperature

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Crop Responses to Elevated Carbon Dioxide and Interaction with Temperature: Grain Legumes

P. V. Vara Prasad
L. H. Allen, Jr.
K. J. Boote

SUMMARY. Atmospheric carbon dioxide concentration ($[\text{CO}_2]$) and other greenhouse gases have risen over the past few decades. If this continues, it could indirectly lead to increases in global temperature. Responses of grain legume crops (soybean, dry bean, peanut and cowpea) to elevated $[\text{CO}_2]$ and interactions with temperature are summarized. Our research shows that, in the absence of biotic (pests, diseases and

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weeds) or abiotic (temperature, water and nutrients) stresses, elevated [CO₂] will increase yield due to increased photosynthesis and growth. However, at above optimum temperatures, the beneficial effects of elevated [CO₂] are more than offset by negative effects of temperature on yield and yield-components, leading to lower seed yield and poor seed quality. Future research should focus on developing genetic and agronomic crop management practices to improve crop productivity under changing climates. [Article copies available for a fee from The Haworth Document Delivery Service: 1-800-HAWORTH. E-mail address: <docdelivery@haworthpress.com> Website: <<http://www.HaworthPress.com>> © 2005 by The Haworth Press, Inc. All rights reserved.]

KEYWORDS. Carbon dioxide, temperature, climate change, global warming, legumes, photosynthesis, respiration, water use efficiency, growth, yield, seed quality

ABBREVIATIONS. Atmospheric carbon dioxide concentration [CO₂], Soil Plant Atmospheric Research (SPAR), Water Use Efficiency (WUE), Carbon Exchange Rate (CER), Leaf Photosynthetic Assimilation Rate (A), Leaf Area Index (LAI), Total Nonstructural Carbohydrates (TNC), Ribulose Biphosphate Carboxylase-Oxygenase (Rubisco), Ribulose Biphosphate (RuBP)

INTRODUCTION

Legumes are important components of cropping systems and are major sources of vegetable oil and protein for human and animal consumption. They provide about 20% of the world's protein for human diet, and one-fourth of the world's fats and oils (Harlan, 1992). Legumes also help to enrich soil through their unique capability to form symbiotic relationships with nitrogen-fixing bacteria that capture atmospheric nitrogen and make it available for crop growth. In addition, legumes are traditionally used as green manure and cover crops in crop rotation to improve soil physical conditions. Legumes belong to the family Leguminosae, subfamily Papilionoideae, and are by far the plant family most utilized by humans in terms of numbers of genera and species. The legume family contains about 650 genera and 18,000 species. This chapter will focus on soybean [*Glycine max* (L.) Merr.], dry bean (*Phaseolus vulgaris* L.), peanut (*Arachis hypogaea* L.), and cowpea [*Vigna unguiculata* (L.) Walp.]. These four grain (seed) legume crops are widely cultivated across the world under a wide range of climatic conditions. Details on origin and pro-

duction statistics of these crops are given in Table 1. Grain legume crops are commonly referred to as pulse crops in Southeast Asia and Australia.

In the recent years $[\text{CO}_2]$ has rapidly increased to about $370 \mu\text{mol mol}^{-1}$ at present. At present rates of emissions, $[\text{CO}_2]$ is predicted to more than double by the end of 21st century (Houghton et al., 2001). These changes in atmospheric $[\text{CO}_2]$ along with other greenhouse gases (water vapor, methane, nitrous oxide, sulphur dioxide) can potentially change global climate. At the present rate of CO_2 increase, various atmospheric general circulation models have predicted that the near-surface temperature of the earth could increase as much as 3 to 6°C (Houghton et al., 2001).

Changes in $[\text{CO}_2]$ and associated changes in global temperature can cause significant changes in crop production. In this review, we will summarize the responses of soybean, dry bean, peanut and cowpea to elevated $[\text{CO}_2]$ and its interaction with temperature. Among all the legume crops, soybean is the most widely studied crop species with reference to responses to elevated $[\text{CO}_2]$. Because of the breadth of available literature, most of the examples are drawn from soybean; however, species differences between these legume crops will be highlighted and discussed as necessary.

CONTROLLED ENVIRONMENT FACILITIES AND EXPERIMENTAL DETAILS

Over the past two decades, considerable research on CO_2 responses of grain crops was conducted in the sunlit, controlled environment chambers known as

TABLE 1. Origin, total world harvested area and production during 2001 (FAO, 2001) and important countries producing soybean, dry bean, peanut and cowpea.

Crop	Origin	Harvested area (Million ha)	Total production (Million tons)	Important countries
Soybean	Northern China	75.5	176.6	USA, China, Argentina, Brazil and India
Dry bean	Central and/or South America	23.2	16.8	India, Brazil, China, Myanmar, Mexico
Peanut	Argentina and/or Bolivia	25.5	35.1	India, China, Nigeria, Senegal, USA
Cowpea	West Africa and/or India	9.9	3.0	Nigeria, Niger, Myanmar

Soil-Plant-Atmosphere-Research (SPAR) chambers at the University of Florida, Gainesville, Florida, USA. A list of grain legumes experiments conducted in the SPAR facility is given in Table 2. Details of the chamber characteristics and functions, methods and quality of specific chamber environment, control are described in several publications (Jones et al., 1984; Baker et al., 1989; Pickering et al., 1994; Prasad et al., 2002). In brief, SPAR growth chambers are located outdoors and use solar radiation as light source. Each chamber has two parts, the upper chamber measures 1 m wide, 2 m long and 1.5 m high and is made of aluminum frame work with polyethylene telephthalate “six light” film walls. The bottom rooting-chamber (aluminum lysimeter) has the same cross section and is 0.6 m deep to accommodate the rooting medium. Each chamber has the capability to control air temperature and dewpoint temperature and [CO₂] at given set points. Air is circulated from top to bottom of the canopy chamber using fans located in external ductwork. The air handling system consists of a chilled water heat exchanger and electrical resistive heater coils.

Dry bulb air temperatures were measured with aspirated and shielded copper-constantan thermocouples and controlled by turning on and off the electrical resistance proportional heaters located in the exits ductwork. Air dewpoint temperatures were measured using hygrometers and controlled by opening and closing bypass valves that determine the flow of chilled water through the cooling coils. The condensate from each cooling coil was collected by a tip-

TABLE 2. Treatment details of experiments on grain legumes conducted in SPAR growth chambers at the University of Florida, Gainesville, USA.

Year	Crop	Carbon dioxide concentration ($\mu\text{mol mol}^{-1}$)	Diurnal temperature (maximum/minimum °C)
1980	Soybean	320, 640	31/23
1981	Soybean	330, 450, 600, 800	31/23
1982	Soybean	330, 450, 600, 800	31/23
1983	Soybean	330, 660	31/23
1984	Soybean	160, 220, 280, 330, 660, 990	31/23
1985	Soybean	330, 660	31/23
1985	Soybean	330, 660	26/19, 31/24, 36/29
1993	Soybean	350, 700	28/18, 32/22, 36/26, 40/30
1994	Soybean	350, 700	28/18, 32/22, 36/26, 40/30, 44/34, 48/38
2000	Dry bean	350, 700	28/18, 31/21, 34/24, 37/27, 40/30
2002	Peanut	350, 700	32/22, 34/24, 40/30, 44/34

ping bucket rain-gauge to estimate evapotranspiration at 5 min intervals. In most of the experiments, plants were grown throughout the season at a range of pre-set $[\text{CO}_2]$ and/or temperature regimes. Air temperature and dewpoint temperature were typically controlled according to a sinusoidal wave function during the day and a decay function during the night. Dewpoint temperatures were maintained 10°C below target dry bulb air temperature. The temperatures indicated in this chapter are the daytime maximum and nighttime minimum temperature, unless stated otherwise.

Daytime $[\text{CO}_2]$ was measured by drawing samples from the chamber every 10 s and controlled at given set points by injecting pure CO_2 from a high pressure cylinder through a mass flow controller. $[\text{CO}_2]$ was not controlled during nighttime and vents were used to remove excess CO_2 due to respiration every hour. The carbon exchange rates were estimated from CO_2 injection rate and the change in $[\text{CO}_2]$ after correcting for leakage in the chamber. Incoming solar radiation was measured using a pyranometer or solar cells. Canopy temperature was measured using infrared sensors. Measurements of all parameters were taken every 10 s, means were stored at 5-min intervals, and all data were downloaded automatically to a computer every night.

Leaf-level photosynthesis, stomatal conductance, and transpiration were measured on individual attached leaves using a LICOR 6200 photosynthesis system. Phenology, growth and dry matter production data were collected at frequent time intervals. At each harvest, plant height, vegetative stage, leaf area, and dry weights of components parts (leaf, stem, root, pod and seed) were recorded. At maturity, final yield, biomass production, partitioning, and yield component were measured either from a sub-sample of plants or on a land area basis. For detailed methods see individual references.

In most experiments, temperature and $[\text{CO}_2]$ treatments were started from emergence to maturity, unless indicated otherwise. Crops were grown under optimal crop management practices with no water or nutrient stress. Irrigation was provided by subsurface irrigation and/or overhead sprinklers as necessary. Crops were kept weed free by regular hand weeding and insect and disease problems were controlled by appropriate chemical sprays as necessary.

EFFECTS OF $[\text{CO}_2]$

Carbon and Water Use Efficiency

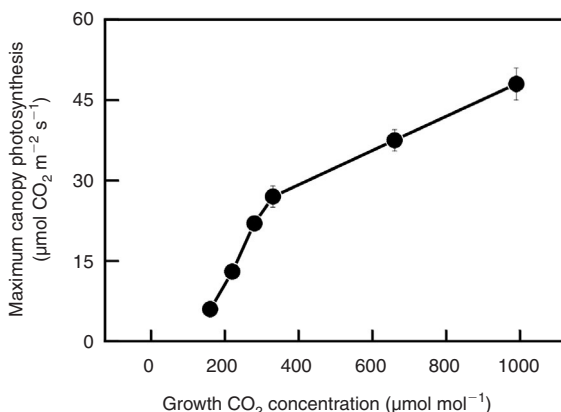
Photosynthesis

Current atmospheric $[\text{CO}_2]$ is sub-optimal for photosynthesis of C_3 plant species including soybean, dry bean, peanut and cowpea. In C_3 species, the

primary acceptor of CO_2 is ribulose biphosphate (RuBP) and the enzyme that catalyzes this reaction is ribulose biphosphate carboxylase-oxygenase (Rubisco). As Rubisco catalyzes both carboxylation and oxygenase reactions, CO_2 and O_2 compete for the same site on Rubisco. The oxygenase activity of Rubisco (photorespiration) leads to $\approx 25\%$ (20 to 60%) loss of carbon in C_3 species (Bowes, 1996). Due to competitive interaction, increase in $[\text{CO}_2]$ will diminish the oxygenase activity of O_2 . Therefore, doubling the current $[\text{CO}_2]$ will increase carboxylation, decrease oxygenation and photorespiration, and thus will increase the rate of net photosynthesis of C_3 species by about 30 to 40% (Bowes, 1996).

Photosynthetic rates of soybean were increased by elevated $[\text{CO}_2]$ at both leaf (Vu et al., 1997, 2001) and canopy levels (Jones et al., 1984a, 1985a; Allen et al., 1987). Increased photosynthetic rates were observed with both short-term and long-term exposures to elevated $[\text{CO}_2]$ (Valle et al., 1985a; Campbell et al., 1990). Maximum midday photosynthetic rates of soybean canopies during periods of peak irradiance ($1,100$ to $1,370 \mu\text{mol photons m}^{-2} \text{s}^{-1}$), showed a strong positive response to growth $[\text{CO}_2]$ (Figure 1). Furthermore, photosynthetic rates of soybean plants grown at high $[\text{CO}_2]$ were greater compared to those at $330 \mu\text{mol mol}^{-1}$ at all levels of irradiance ranging from 100 to $1200 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ (Campbell et al., 1988; 1990). Increased photosynthetic rates of soybean leaves and/or canopies with elevated $[\text{CO}_2]$ have been reported in several other studies (Huber et al., 1984; Hesketh et al.,

FIGURE 1. Maximum midday photosynthetic rates (measured when solar irradiance was between $1,100$ and $1,370 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) on land area basis of soybean canopies grown and measured at different $[\text{CO}_2]$. (Adapted from Campbell et al., 1990.)

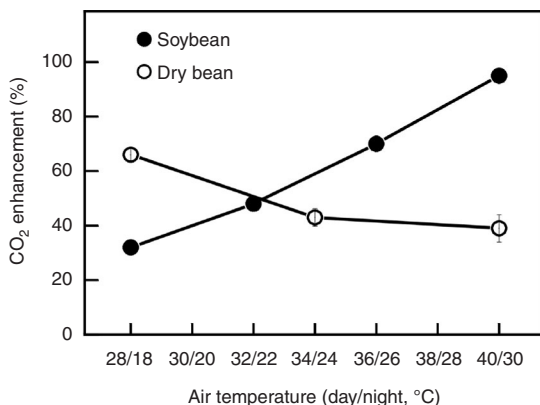


1984; Sionit et al., 1984; Chen et al., 1995; Ferris et al., 1998; Ziska et al., 2001). An increase in daytime canopy photosynthesis rates at elevated $[\text{CO}_2]$ was observed at both vegetative and reproductive stages (Jones et al., 1985a and b). However, crop canopy photosynthetic rates can vary throughout the growing season mainly due to different requirements of photo-assimilates (Acocck et al., 1985).

Campbell et al. (1988) measured Rubisco activity and amount in soybean leaves grown at a range of sub and super-ambient $[\text{CO}_2]$ and found that Rubisco activity was almost constant ($1.0 \mu\text{mol CO}_2 \text{ min}^{-1} \text{ g}^{-1}$ soluble protein) mainly because leaf soluble protein was nearly constant (2.4 g m^{-2}) with 55% being Rubisco protein. In contrast, Rubisco activity expressed on a leaf dry weight basis decreased because of an increase in specific leaf weight with an increase in $[\text{CO}_2]$. Campbell et al. (1990) also showed that photosynthetic capacity of soybean canopies grown at 330 and $660 \mu\text{mol mol}^{-1}$ of $[\text{CO}_2]$ were similar for short exposures at $[\text{CO}_2]$ below $550 \mu\text{mol mol}^{-1}$, but above this value, canopies grown at $660 \mu\text{mol mol}^{-1}$ had a higher photosynthetic capacity. Vu et al. (1989) suggested that an increase in starch storage sites due to an increased number of palisade cells, together with the maintenance of Rubisco activity, enables soybean to continue to exhibit high photosynthetic rates throughout the growth period under high $[\text{CO}_2]$. This suggests that photosynthetic capacity of soybean was not down regulated at elevated $[\text{CO}_2]$. Similar responses were observed in most of our studies on soybean. Allen et al. (1996), attributed this response to the typical characteristics of the soybean crop, which include: (i) high symbiotic N_2 fixation capability; (ii) the capacity to form an additional layer of palisade cells in the leaf tissue; (iii) the capacity to shunt much of the photoassimilates into relatively inert starch rather than soluble sugars during photosynthesis; (iv) a relatively strong leaf and stem sink during vegetative development; and (v) a strong seed sink during reproductive development. Plants that lack these capacities, either inherently or because of growth in limiting environments, are more likely to demonstrate some degree of down regulation of photosynthesis (Allen, 1994).

In dry bean, growth at elevated $[\text{CO}_2]$ increased leaf photosynthetic rates (Figure 2; Prasad et al., 2002). This agrees with Sage (1994) who reported an increase in net CO_2 assimilation rates by about 30%. Similarly, growth at sub-ambient $[\text{CO}_2]$ ($200 \mu\text{mol mol}^{-1}$) compared with near ambient $[\text{CO}_2]$ ($380 \mu\text{mol mol}^{-1}$) decreased net assimilation rates by 40% at $25/20^\circ\text{C}$ (Cowling and Sage, 1998). In contrast, Socias et al. (1993) found that photosynthetic rates of dry bean plants grown at 350 and $650 \mu\text{mol mol}^{-1}$ of $[\text{CO}_2]$ were similar, when measured at the growth $[\text{CO}_2]$. Furthermore, the rate of RuBP consumption was lower in plants grown at elevated $[\text{CO}_2]$, but the $[\text{CO}_2]$ at which maximum consumption occurred was higher in plants grown in high $[\text{CO}_2]$, indicating acclimation to high $[\text{CO}_2]$. This acclimation of RuBP consumption

FIGURE 2. Carbon dioxide enhancement (%) in leaf photosynthetic rates due to twice-ambient $[\text{CO}_2]$ ($700 \mu\text{mol mol}^{-1}$) of soybean and dry bean leaves grown and measured at different growth temperatures. (Redrawn from Vu et al., 1997 and Prasad et al., 2002.)



was related to a decrease in Rubisco activity resulting from decreased carbamylation, not a loss of Rubisco protein. Similarly, leaves of dry bean plants grown in enriched CO_2 ($1,400 \mu\text{mol mol}^{-1}$) showed a decrease in CO_2 exchange capacity compared with leaves grown in ambient $[\text{CO}_2]$ ($340 \mu\text{mol mol}^{-1}$), when measured at the same $[\text{CO}_2]$ (Ehret and Jolliffe, 1985). Acclimation of photosynthesis to elevated $[\text{CO}_2]$ with decreases in Rubisco activity was reported by Sage et al. (1989). These differential responses could be related to growth conditions and nutrient stress. In the later two studies, dry bean plants were grown in small pots, i.e., 3 L (Socias et al., 1993) and 0.85 L (Ehret and Jolliffe, 1985), while those by Prasad et al. (2002) were grown in 2 m long, 1 m wide and 0.6 m deep lysimeter and by Sage (1994) in 20 L pots. The effects of restricted pot volume on photosynthetic acclimation are well documented (Arp, 1991). Sage (1994) compared the ratios of net CO_2 assimilation rates of plants grown at elevated and ambient $[\text{CO}_2]$ obtained from four independent studies on dry bean and soybean, where plants were grown in different size pots. In both species, pot size had pronounced effects on net CO_2 assimilation rates (A). Plants grown in small pots (<5 L) exhibited carbon assimilation ratios (i.e., A at elevated CO_2 /A at ambient CO_2) less than one across a wide range of intercellular $[\text{CO}_2]$ (C_i) between 100 to $900 \mu\text{mol mol}^{-1}$. In contrast, the carbon assimilation ratio of plants grown in large 20 L pots or in field experiments was not affected or enhanced by CO_2 enrichment across a range of C_i . Radogalou et al. (1992) found that the net photosynthetic rate of dry bean leaves grown in high nutrient levels did not show a down-reg-

ulation under elevated $[\text{CO}_2]$. Mjwara et al. (1996) reported that CO_2 enrichment ($700 \mu\text{mol mol}^{-1}$) compared to ambient ($360 \mu\text{mol mol}^{-1}$) increased carbon assimilation rates of bean early in the season, but from 20 days after germination there was a steady decline to almost similar levels to those measured in plants grown under ambient $[\text{CO}_2]$. This clearly suggests that acclimation response varies with the growth environment, age, nutrient status of the soil, and ability of plant roots to grow in an unrestricted volume.

The possible mechanisms for differential responses to elevated $[\text{CO}_2]$ in small pots could be attributed to the following: (i) accumulation of greater nonstructural carbohydrates in plants grown in small pots or under nutrient deficiency (Robbins and Pharr, 1988) which in turn can lead to feedback inhibition of photosynthesis (Stitt, 1991; Bowes, 1996); (ii) plants exposed to elevated $[\text{CO}_2]$ have greater initial growth rates and become nutrient-limited earlier than those grown in ambient $[\text{CO}_2]$ (Coleman et al., 1993); (iii) root crowding and resistance to root expansion in small pots leads to release of abscisic acid and other signals that inhibit photosynthesis (Tardieu and Davis, 1993); and (iv) root tip damage due to desiccation at the bottom of the pots, which can trigger the release of large amounts of inhibitory chemicals which reduce stomatal conductance and lead to hormonally-controlled restrictions of shoot expansion, and lower sink capacity of leaves (Zhang and Davies, 1987; Davies et al., 1990). These mechanisms are discussed in detail by Sage (1994).

Elevated $[\text{CO}_2]$ increased net photosynthesis and light saturated carbon assimilation rates of peanut under both irrigated and drought conditions (Clifford et al., 1993, 2000; Stronach et al., 1994). Clifford et al. (1993) reported a 40% increase in maximum leaf photosynthetic rate in peanut. Chen and Sung (1990) observed that when peanut plants were exposed to elevated $[\text{CO}_2]$ ($1,000 \mu\text{mol mol}^{-1}$) starting from pod formation to maturity, there was an increase in soluble protein content and Rubisco, and plants even showed upregulation of photosynthesis and internal $[\text{CO}_2]$ response (A:Ci) curve. Valle et al. (1985a) reported that soybean leaves grown at elevated $[\text{CO}_2]$ had higher A_{max} with respect to saturating $[\text{CO}_2]$. Such responses are likely to be associated with increases in specific leaf weight under elevated $[\text{CO}_2]$ (Vu et al., 1989). Increases in leaf photosynthetic rates were also reported in cowpea (Lopez et al., 1987; Overdieck et al., 1988; Ahmed et al., 1993).

Respiration

Amthor (1991, 1997) suggested that the response of respiration to CO_2 enrichment can be described in terms of effects of instantaneous or current $[\text{CO}_2]$ (direct effects) or those related to CO_2 -history of plants (indirect effects). Examples of indirect effects include differences in respiration caused by CO_2 -induced changes in carbohydrate or protein concentration of the plant. Thomas

and Griffin (1994) studied soybean leaf respiration in response to $[\text{CO}_2]$ and found that effects were variable and dependent on both the basis on which the respiration was expressed and the extent of leaf expansion (leaf age). Respiration rates of expanding leaves were not affected by growth $[\text{CO}_2]$, whereas CO_2 enrichment significantly increased respiration in fully expanded leaves when rates were expressed on either a leaf area basis (+ 27%), total non-structural carbohydrate basis (+ 35%) or leaf N basis (+ 42%). Contrasting results were found when respiration was expressed on a leaf dry mass basis. Respiration rates of fully expanded leaves were not significantly affected by growth $[\text{CO}_2]$, but expanding leaves had a 19% lower respiration rate under elevated $[\text{CO}_2]$ than under ambient $[\text{CO}_2]$. Similar responses were observed in several plant species (Gifford et al., 1985; Bunce and Caulfield, 1991). Thomas and Griffin (1994) partitioned total respiration into the components contributing to the formation of new tissues (growth respiration) and to the maintenance of existing tissues (maintenance respiration). They found that elevated $[\text{CO}_2]$ did not affect growth respiration but increased maintenance respiration (+ 34%), which was correlated to with high leaf carbohydrate levels (+ 33%). Boote et al. (1997) suggested that the lower respiration rates expressed on unit tissue mass (specific respiration rate) could be attributed to indirect effects of elevated $[\text{CO}_2]$ associated with: (i) shifts in composition with more carbohydrate and less protein causing lower synthesis cost, (ii) increase in structure-support components that are lower in synthesis and maintenance cost, and (iii) lower protein causing lower maintenance respiration.

Results of respiration studies differ with the experimental methodology used to measure CO_2 efflux, i.e., closed or open system (Long and Hallgren, 1993; Drake et al., 1999; Amthor, 1997). Preliminary studies conducted by Jahnke (2001) on dry bean showed that inhibition of dark CO_2 efflux by elevated $[\text{CO}_2]$ was found using an open gas exchange system; but when the same leaf was investigated in a closed system, no such inhibition was detected. Jahnke (2001) conducted detailed experiments on dry bean in a specialized gas exchange system in three different ways: (i) as a closed system in which $[\text{CO}_2]$ increased continuously from 200 to 4,200 $\mu\text{mol mol}^{-1}$ due to respiration of the enclosed leaf; (ii) as an intermittently closed system that was repeatedly closed and opened during $[\text{CO}_2]$ period of either 350 or 2,000 $\mu\text{mol mol}^{-1}$; and (iii) as an open system in which $[\text{CO}_2]$ varied between 350 and 2,000 $\mu\text{mol mol}^{-1}$. As a control, respective system characteristics were evaluated carefully in an empty leaf chamber. It was observed that when all the relevant system characteristics were taken into account, no effects of short-term changes in CO_2 on dark CO_2 efflux of dry bean leaves were found, even when $[\text{CO}_2]$ increased to 4,200 $\mu\text{mol mol}^{-1}$. It was concluded that the leaf respiration of dry bean is not directly inhibited by elevated $[\text{CO}_2]$ (Jahnke, 2001). Jahnke and Krewitt (2002) reported older leaves of tobacco which has

homobaric leaf anatomy (intercellular air spaces are not compartmented and have a continuous system of open pores) can lead to internal leakage and give a false indication of leaf respiration rates being decreased in elevated $[\text{CO}_2]$ chambers. When internal leakage was experimentally restricted, the CO_2 inhibition on CO_2 efflux was no longer observed. They concluded that a true direct effect of $[\text{CO}_2]$ on leaf respiration does not exist and direct effects of CO_2 on dark respiration reported in the literature might be artifactual (Jahnke and Krewitt, 2002). However, further research is needed across other crop species to confirm these. Clearly Thus, the variable response of respiration to elevated $[\text{CO}_2]$ may be attributed to age of the leaf, period of exposure, method of measurement, units of measurement and expression and defects if measurement techniques. Further research is needed to understand the effects of elevated $[\text{CO}_2]$ on growth and maintenance respiration of various component parts including leaves and roots.

Stomatal Conductance, Transpiration, and Water Use Efficiency

One of the most important phenomena responsive/sensitive to increasing $[\text{CO}_2]$ levels is partial stomatal closure. A recent review on soybean showed that stomatal conductance was decreased by 31% at 450-550 $\mu\text{mol mol}^{-1}$ $[\text{CO}_2]$, 36% at 600-800 $\mu\text{mol mol}^{-1}$, and 51% at $> 850 \mu\text{mol mol}^{-1}$ of $[\text{CO}_2]$ with respect to ambient 330-360 $\mu\text{mol mol}^{-1}$ $[\text{CO}_2]$ (Ainsworth et al., 2002). Similarly, a previous review of soybean reported a 30% decrease in stomatal conductance with a doubling of $[\text{CO}_2]$ (Cure, 1985; Cure and Acock, 1986). In addition to decreased stomatal conductance, partial stomatal closure increases leaf resistance to transpirational water loss resulting in lower leaf transpiration rates. This may lead to an increase in leaf or tissue temperatures. In controlled environments, foliage temperatures of soybean grown at 700 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ were 1 to 2°C warmer compared to those grown at 350 $\mu\text{mol mol}^{-1}$ (Campbell et al., 1990). Similar increases were observed in dry bean (Prasad et al., 2002). As leaf temperature increases, the vapor pressure inside the leaves will increase leading to a higher leaf-to-air vapor pressure difference, which is the driving force for transpiration leading to increased transpiration rate per unit leaf area and thus maintain those rates at slightly lower values than would exist at ambient $[\text{CO}_2]$.

Valle et al. (1985b) reported that diurnal transpiration rates of soybean leaflets grown and measured at high (660 $\mu\text{mol mol}^{-1}$) and ambient (330 $\mu\text{mol mol}^{-1}$) $[\text{CO}_2]$ were almost similar. This is mainly because the increases in leaf resistance caused by high $[\text{CO}_2]$ were partially offset by increases in vapor pressure gradient between leaves to air caused by increases in leaf temperatures (Table 3). Effects of changes in leaf conductance to elevated $[\text{CO}_2]$ on single leaf transpiration cannot be directly transferred to transpiration from

TABLE 3. Carbon exchange rate (CER), transpiration rate (TR), leaf temperature (TL), leaf resistance (rL), vapor pressure gradient (VPG), water-use efficiency (WUE), air temperature (Ta) and air vapor pressure (VP_a) at midday (1130-1230 h EST) of soybean leaves grown and measured at ambient (330 μmol mol⁻¹) and high (660 μmol mol⁻¹) [CO₂]. (Adapted from Valle et al., 1985b.)

Parameter	Carbon dioxide concentration (μmol mol ⁻¹)	
	330	660
CER (μmol m ⁻² s ⁻¹)	21.2	41.1*
TR (mmol m ⁻² s ⁻¹)	5.46 ± 0.19†	5.17 ± 0.11
TL (°C)	30.7 ± 0.30	32.5 ± 0.50
rL (s m ⁻²)	146 ± 6.50	187 ± 5.00*
VPG (10 ² Pa)	19.9 ± 0.80	24.3 ± 1.60
WUE (mmol mol ⁻¹)	3.9 ± 0.10	7.9 ± 0.20*
Ta (°C)	29.3 ± 0.13	29.9 ± 0.23
VPa (10 ² Pa)	20.7 ± 0.17	20.9 ± 0.24

* Significant at P < 0.05 t-test; comparison within rows
† Average of four leaves ± standard error; n = 24 for 330 and 21 for 660 μmol mol⁻¹

whole crop canopies under field conditions. Comparison of transpiration rates of soybean canopies grown at high (800 μmol mol⁻¹) versus ambient (330 μmol mol⁻¹) [CO₂] (corresponding LAI values were 6.0 to 3.3, respectively) showed that changes in transpiration rates were in the range of -2% (Jones et al., 1985a) to +11% (Jones et al., 1985b). In another experiment, where soybean canopies grown at ambient (330 μmol mol⁻¹) and high (700 μmol mol⁻¹) [CO₂] had similar LAI (about 3.4), the seasonal cumulative water use was decreased by 12% at high [CO₂] (Jones et al., 1985c).

In some studies, total canopy water use of soybean was reduced by [CO₂] enrichment (Jones et al., 1985 c; Rogers et al., 1984), while in others it was unaffected (Jones et al., 1985a; Kimball et al., 1984). Albeit to partial stomatal closure, water use per unit leaf area is reduced, much of this reduction in transpiration is offset due to greater LAI increases at elevated [CO₂]. Even at similar LAI, the canopy energy balance would cause foliage temperature to rise and prevent full expression of reduction effects of stomatal conductance on transpiration as indicated above.

Water use efficiency (WUE) is defined as the ratio of the quantity of plant production to the quantity of the water transpired, evaporated or consumed. It can be described in terms of dry matter production, grain yield, or CO₂ uptake. For example, photosynthetic WUE is defined as a ratio of the photosynthetic

carbon exchange rate to transpiration and can be expressed on a leaf area, whole-canopy, or ground area basis. Similarly, whole season WUE is best defined as the ratio of total dry matter (or seed yield) produced to total amount of water used by the crop. Based on the above definitions an increase in WUE can be obtained from increased carbon exchange rate and dry matter production, or from decreased transpiration and total water use.

Allen et al. (1985) compared WUE of soybean canopies grown at 330 and 800 $\mu\text{mol CO}_2 \text{ mol}^{-1}$, with an LAI of 3.3 and 6.0, respectively. In each of the two treatments, $[\text{CO}_2]$ levels were cross-switched for one day. The ratio of the WUE (i.e., WUE at 800 ppm $[\text{CO}_2]$ divided by the WUE at 330 $\mu\text{mol mol}^{-1}$) averaged 2.33. The relative contributions of photosynthesis and transpiration to the ratio of WUE were 73 and 27%, respectively. These comparisons are valid as the same canopy was used for both $[\text{CO}_2]$ concentrations. Exposure to elevated $[\text{CO}_2]$ increased water use efficiency, mainly due to increased carbon exchange rates (Table 3).

Clifford et al. (2000) observed that stomatal conductance and transpiration rate of peanut were decreased under elevated $[\text{CO}_2]$ in both irrigated and drought conditions. These reductions in combination with a relative delay in decline in relative water content, leaf water potential and turgor potential can lead to an increase in seasonal water use efficiency in peanut (Stronach et al., 1994). Decreases in stomatal conductivity and transpiration rates at elevated $[\text{CO}_2]$ were reported in other studies on peanut (Chen and Sung, 1990; Clifford et al., 1995), dry bean (Radoglou et al., 1992; Prasad et al., 2002) and cowpea (Morison and Gifford, 1984).

Allen (1999) concluded that although stomatal conductance may be decreased by about 40% for doubled $[\text{CO}_2]$, water use by C_3 crops under field conditions will probably be decreased only by up to 12%. If increases in leaf area due to doubled $[\text{CO}_2]$ are small (or can be controlled), then the transpiration reductions would be meaningful, albeit small. If increases in leaf area due to doubled $[\text{CO}_2]$ are large, then no reductions in transpiration would be expected, and even small increases might be possible.

Phenology, Growth, Yield, and Seed Quality

Phenology

Allen et al. (1990) studied the effects of $[\text{CO}_2]$ on soybean developmental stages and expansive growth over four years and concluded that vegetative stages progressed slightly faster and the final number of nodes was slightly greater with increased $[\text{CO}_2]$. Time to reproductive stages was similar across the range of $[\text{CO}_2]$ (160 to 990 $\mu\text{mol mol}^{-1}$), however, plants grown at 160 $\mu\text{mol mol}^{-1}$ $[\text{CO}_2]$ lagged behind plants grown at other $[\text{CO}_2]$'s at the begin-

ning of flowering, but after 52 days, plants in all treatments had reached the same reproductive stage (Allen et al., 1991). In contrast, earlier studies showed that above-ambient $[\text{CO}_2]$ either had no effect (Allen et al., 1988), decreased (Baker et al., 1989; Allen et al., 1990), or increased time to flowering (Rogers et al., 1984; Ellis et al., 1995). There was no effect of elevated $[\text{CO}_2]$ on time to flowering or maturity for dry bean (Prasad et al., 2002). In cowpea, Bhattacharya et al. (1985) and Ellis et al. (1995) reported hastening of flowering by CO_2 enrichment, while Ahmed et al. (1993) reported no effect of CO_2 enrichment on time to first flowering.

Organ Growth and Partitioning

Allen et al. (1991) grew soybean from planting to maturity in a wide range of sub-ambient and super-ambient $[\text{CO}_2]$ and acquired time series data on dry matter accumulation and leaf area. Responses of dry matter accumulation to $[\text{CO}_2]$ during the linear phase were fitted by an empirical nonlinear regression model. A rectangular hyperbola of a modified Michaelis-Menten equation given below was adapted to model the response as a function of $[\text{CO}_2]$ (Allen et al., 1987).

$$Y = \beta_0 + \beta_1 (DAP - D)(C - G)/(C - Kc)$$

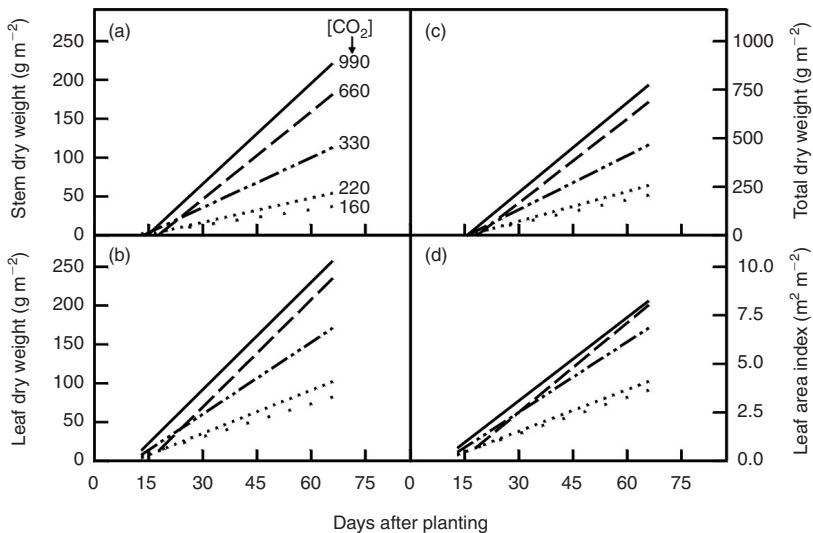
where Y = dependent growth variable (dry weight or leaf area); β_0 = intercept on Y -axis when second term is zero; β_1 = maximum asymptotic value of dry matter or leaf area growth rate when $[\text{CO}_2]$ is no longer limiting; D = days after planting (DAP) offset parameter to remove the time lag between seedling emergence and nonlinear early plant growth; $C = [\text{CO}_2]$; G = apparent $[\text{CO}_2]$ compensation point for the dependent variable; and Kc = hyperbolic function shape factor, related to the apparent Michaelis constant. Allen et al. (1991) concluded that growth rates of all plant parts during the linear phase of growth (24 to 66 DAP) were stimulated by elevated $[\text{CO}_2]$ (Table 4). This resulted in greater dry weights of all of the various component parts (Figure 3). The relative ranking of the $[\text{CO}_2]$ treatment effect on growth rates among different plant parts was stem > petiole > leaf biomass > leaf area (Table 4).

Initiation and expansion of leaves on both the main stem and branches were faster in soybean plants grown at elevated $[\text{CO}_2]$ compared to ambient $[\text{CO}_2]$ (Cure et al., 1988). Allen et al. (1990) reported that expansive soybean growth increased with $[\text{CO}_2]$, leading to greater mainstem height, branch lengths, stem diameter, individual leaf area and leaf area per plant. An increase in mainstem height was attributed to increased node number and stimulation of internode elongation (Rogers et al., 1984; Allen et al., 1990). Furthermore, in-

TABLE 4. Growth rates of different plant component during the linear phase of growth (24 to 66 days after planting) of soybean plants grown at sub-ambient, ambient and super-ambient $[\text{CO}_2]$. (Adapted from Allen et al., 1991.)

Parameter	Carbon dioxide concentration ($\mu\text{mol mol}^{-1}$)					
	160	220	280	330	660	990
Total shoot dry weight ($\text{g m}^{-2} \text{ day}^{-1}$)	5.0	8.4	10.9	12.5	18.2	20.7
Stem dry weight ($\text{g m}^{-2} \text{ day}^{-1}$)	0.8	1.7	2.4	2.9	4.7	5.5
Petiole dry weight ($\text{g m}^{-2} \text{ day}^{-1}$)	0.5	1.0	1.4	1.6	2.5	2.9
Leaf dry weight ($\text{g m}^{-2} \text{ day}^{-1}$)	1.7	2.7	3.4	3.9	5.3	5.8
Leaf area ($\text{m}^2 \text{ m}^{-2} \text{ day}^{-1}$)	0.07	0.12	0.14	0.15	0.19	0.20

FIGURE 3. Component dry weights of different component parts of soybean plants grown at different $[\text{CO}_2]$ during the linear phase from 13 to 66 days after planting. (Redrawn from Allen et al., 1991.)



creases in extension rates of branches were greater than of mainstems under elevated $[\text{CO}_2]$ (Allen et al., 1990).

Partitioning of photoassimilates to various plant organs of soybean over time was influenced by $[\text{CO}_2]$. Plants grown at sub-ambient $[\text{CO}_2]$ partitioned carbon preferably to leaves, which served to increase carbon fixation capabil-

ity, while plants grown at super-ambient $[\text{CO}_2]$ partitioned more carbon to supporting structures such as stems, petioles and roots than to leaf laminae, especially during the vegetative stages (Allen et al., 1991). This mechanism could be for balancing the supply and demand for carbohydrates needed by the whole plant for balanced growth (Acock and Allen 1985). Alternatively, larger plants normally produce more supporting structure, so the partitioning to these structures may have been a consequence of plant size and hence an indirect effect rather than the direct consequence of super-ambient $[\text{CO}_2]$. Growth at elevated $[\text{CO}_2]$ increased stem, petiole and leaf dry matter production as well as number of branches (Tables 5 and 6). Elevated $[\text{CO}_2]$ increased the total dry matter production in soybean (Allen et al., 1987, 1991; Baker et al., 1989; Pan, 1996), dry bean (Prasad et al., 2002), peanut (Clifford et al. 1993, 2000), and cowpea (Bhattacharya et al., 1985; Overdieck et al., 1988; Ahmed et al., 1993; Ellis et al., 1995).

Elevated $[\text{CO}_2]$ increased specific leaf weight of soybean (Leadley and Reynolds, 1988; Campbell et al., 1988; Vu et al., 2001). This could be attributed to increased carbohydrate accumulation and/or changes in leaf thickness. In soybean, exposure to elevated $[\text{CO}_2]$ increased the number of palisade cells in an extra layer of cells, which contributed to leaf thickness (Thomas and Harvey, 1983). Plants dependent upon nitrate and those dependent on symbiotic N_2 fixation both responded in a similar manner.

Root Growth and Nitrogen Fixation

Exposure to elevated growth $[\text{CO}_2]$ increased total root dry matter, root volume, and root length (Rogers et al., 1992). There were also significant changes

TABLE 5. Dry weights of component plant parts at final harvest of soybean plants grown at sub-ambient, ambient and super-ambient $[\text{CO}_2]$. (Adapted from Allen et al., 1991.)

Parameter	Carbon dioxide concentration ($\mu\text{mol mol}^{-1}$)		
	160	330	660
Leaf dry weight (g plant^{-1})	2.30	6.09	5.43
Petiole dry weight (g plant^{-1})	0.66	2.19	2.63
Stem dry weight (g plant^{-1})	1.48	4.63	6.42
Pod dry weight (g plant^{-1})	7.98	20.12	24.64
Seed dry weight (g plant^{-1})	5.77	14.86	17.85
Total dry weight (g plant^{-1})	12.88	33.03	39.12
Seed weight (g seed^{-1})	0.128	0.176	0.167

TABLE 6. Numbers of main stem nodes, branches, pods, seeds and seeds per pod at final harvest of soybean plants grown at sub-ambient and super-ambient $[\text{CO}_2]$. (Adapted from Allen et al., 1991.)

Parameter	Carbon dioxide concentration ($\mu\text{mol mol}^{-1}$)		
	160	330	660
Main stem nodes (plant^{-1})	11	14	14
Number of branches (plant^{-1})	4.4	5.6	6.7
Pods on main stem (plant^{-1})	11.3	17.8	15.3
Pods on branches (plant^{-1})	12.8	18.5	34.9
Total pod number (plant^{-1})	24.0	36.3	50.2
Total seed number (plant^{-1})	45.1	84.3	106.7
Number of seeds per pod	1.88	2.32	2.13

in root anatomy with increases in the diameter of the central stele and width of the cortex. However, there were no effects of CO_2 enrichment on total number of roots or number of roots at specific depths. Similar increases in root weight, length and volume were reported for cotton (Prior et al., 1994; Reddy et al., 1997).

A direct effect of increased root growth and mass due to elevated $[\text{CO}_2]$ in legumes would be on nodulation and microbial activity and thus on biological nitrogen fixation. Increased photosynthetic carbon fixation under elevated $[\text{CO}_2]$ will provide more energy for microbial activity and facilitate nitrogen fixation in legumes. Symbiosis between legume and bacteria was greater under elevated $[\text{CO}_2]$ (Reddy et al., 1989; Reardon et al., 1990). Rogers et al. (1994, 1997) reported that elevated $[\text{CO}_2]$ increased nodule development (i.e., increased nodule dry weight and increased nodule number per plant) and/or nodule function (i.e., increased nitrogenase activity, increased N_2 fixation, and increased whole plant N). Doubling of $[\text{CO}_2]$ resulted in substantial increases in biological nitrogen fixing ability of soybean (Hardman and Brun, 1971; Hardy and Havelka 1973, 1975; Williams et al., 1981). Exposure to elevated $[\text{CO}_2]$ for two weeks increased the number and mass of nodules and nitrogenase activity (Finn and Brun, 1982). However, there was no effect of short-term exposure (48 h) on nitrogenase activity (Finn and Brun, 1982; Williams et al., 1981). Phillips et al. (1976) indicated that in pea long-term CO_2 enrichment promoted N_2 fixation by enhancing nodule development, while short-term increases in $[\text{CO}_2]$ increased N_2 fixation by affecting nodule function. Exposure to high $[\text{CO}_2]$ increased nitrogenase activity in dry bean (Ortega et al., 1992). Kimball (1985), suggested that leguminous crops will

probably not be nitrogen limited in future climates with elevated $[\text{CO}_2]$ any more than they are at present $[\text{CO}_2]$.

Carbohydrate Accumulation

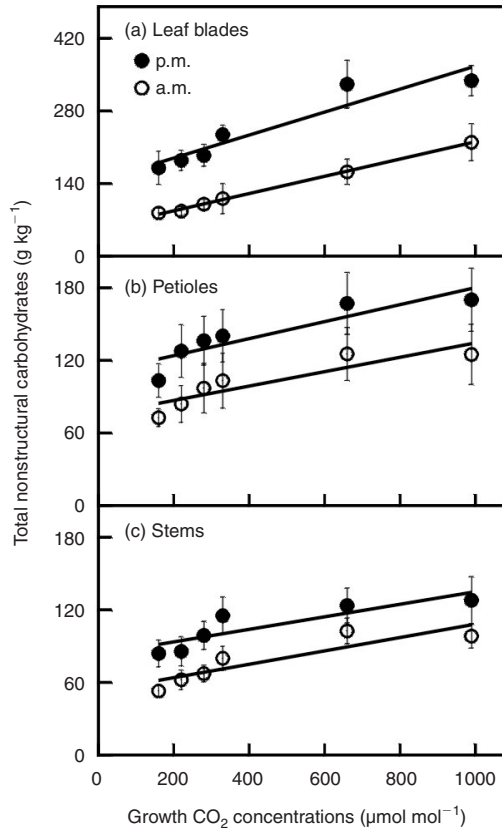
Elevated $[\text{CO}_2]$ increased accumulation of carbohydrates in soybean (Allen et al., 1988; Vu et al., 1989, 1997, 2001), dry bean (Sharkey et al., 1985; Ehret and Jolliffe, 1985), and cowpea (Bhattacharya et al., 1987; Ahmed et al., 1993). Vu et al. (1989) reported linear increases in carbohydrate content and protein concentration of soybean leaves grown across four different $[\text{CO}_2]$ treatments (330, 450, 600 and 800 $\mu\text{mol mol}^{-1}$). Growth at 800 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ significantly increased starch, sucrose, reducing sugars content and concentration chlorophyll and soluble protein compared to plants grown at 330 $\mu\text{mol mol}^{-1}$ of $[\text{CO}_2]$.

Increases in concentrations of total non-structural carbohydrates (TNC) in vegetative tissues due to increased $[\text{CO}_2]$ were also reported at all stages of soybean development (Allen et al., 1998). Linear regression analyses indicated that both morning (a.m.) and evening (p.m.) leaf, petiole and stem TNC concentrations increased with increasing $[\text{CO}_2]$ (Figure 4; Allen et al., 1998). In contrast, there was no significant effect of $[\text{CO}_2]$ on TNC concentrations in pod walls and seeds at any stages of development a feature also confirmed by Thomas (2001). This suggests that individual pods and seeds, once set, are well-buffered and have a limited capacity to respond to $[\text{CO}_2]$. Thus, seed yield response to elevated $[\text{CO}_2]$ is related to other traits such as increase in number of pods (Allen et al., 1991). The fact that plants grown at elevated $[\text{CO}_2]$ contained large amounts of TNC in vegetative parts at maturity indicates that not all the reserves were utilized by seed yield. Therefore, soybean cultivars in the future should be designed to utilize carbohydrates more readily for seed production so that a greater benefit can be realized from rising atmospheric $[\text{CO}_2]$ (Allen, 1994; Allen et al., 1998).

Yield and Yield Components

Several reports showed that increases in $[\text{CO}_2]$ increased seed yields in soybean (Huber et al., 1984; Roger et al., 1986; Cure et al., 1988; Allen et al., 1991), dry bean (Prasad et al., 2002), peanut (Clifford et al., 1993; 2000; Mortley et al., 1997), and cowpea (Ahmed et al., 1993). Ainsworth et al. (2002) summarized the effects of doubled $[\text{CO}_2]$ on soybean yield from 57 different data sets and reported an average increase of 24%. Allen et al. (1987) modeled the response of seed yield to $[\text{CO}_2]$ from experiments conducted at different locations and reported an increase of 32% for doubling of $[\text{CO}_2]$ from 315 to 630 $\mu\text{mol mol}^{-1}$. Similarly, effects of elevated $[\text{CO}_2]$ across five different experiments in Gainesville, Florida showed that doubling of $[\text{CO}_2]$ in-

FIGURE 4. Linear regression of whole-season total nonstructural carbohydrates in (a) leaf blades, (b) petioles, and (c) stems of soybean plants grown at different $[\text{CO}_2]$ at 0800 (a.m.) and 1700 (p.m.) h EST. (Adapted from Allen et al., 1998.)



creased seed yield of soybean by about 35% (Allen and Boote, 2000). Higher seed yields due to elevated $[\text{CO}_2]$ have been shown in other studies (Kimball, 1983; Cure, 1985; Rogers et al., 1986; Ferris et al., 1999; Ziska et al., 2001; Ainsworth et al., 2002). Increases in seed yield at elevated $[\text{CO}_2]$ were mainly attributed to increases in number of pods and seeds from improved branching and greater number of pods on branches (Tables 5 and 6). Harvest index (ratio of seed to total dry matter) decreased at elevated $[\text{CO}_2]$ (Baker et al., 1989; Allen et al., 1991), mainly because CO_2 enrichment causes greater increases in vegetative biomass than in seed yield.

Total dry matter production and pod yields of dry bean increased linearly as $[\text{CO}_2]$ increased from 340 to 1,200 $\mu\text{mol mol}^{-1}$, at which the maximum increase was observed, and further enrichment to 2,000 or 3,000 $\mu\text{mol mol}^{-1}$ had no additional effect (Jolliffe and Ehret, 1985). The percentage of flowers setting seed was lower at elevated $[\text{CO}_2]$ (Figure 5) in spite of greater photosynthetic rates (Figure 2; Prasad et al., 2002). This clearly suggests that reduced seed-set was not a result of decreased availability of photosynthates. The lower seed-set at elevated $[\text{CO}_2]$ may be the result of a greater number of flowers produced due to improved vegetative growth and branching (Jolliffe and Ehret, 1985) or a small shift in tissue temperature at elevated $[\text{CO}_2]$ due to reduced stomatal conductance and transpiration (Matsui et al., 1997; Prasad et al., 2002). CO_2 enrichment increased seed yields of dry bean but did not affect individual seed weight and number of seed per pod at maturity (Figures 6 and 7; Prasad et al., 2002).

CO_2 enrichment increased total dry matter production and pod yield of peanut (Chen and Sung, 1990; Clifford et al., 1993; 2000; Mortley et al., 1997; Stanciel et al., 2000); however, there was no effect of CO_2 enrichment on harvest index (Clifford et al., 1993; Stanciel et al., 2000). Increased seed yield and number of seeds (Bhattacharya et al., 1985; Ahmed et al., 1993) and harvest index (Biswas and Hileman, 1985) were reported in cowpea plants grown under elevated $[\text{CO}_2]$.

FIGURE 5. Effect of temperature on seed-set (proportion of flowers setting seed) of dry bean plants grown at (a) ambient and (b) elevated $[\text{CO}_2]$. Fitted regressions: (a) $Y = 263 + 6.5X$, $r^2 = 0.93$; and (b) $Y = 250 + 6.5X$, $r^2 = 0.93$. (Adapted from Prasad et al., 2002.)

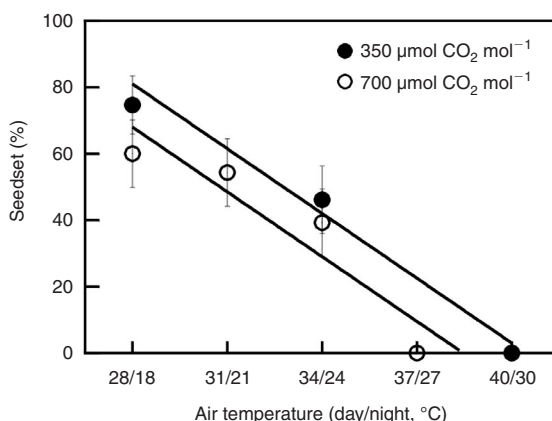
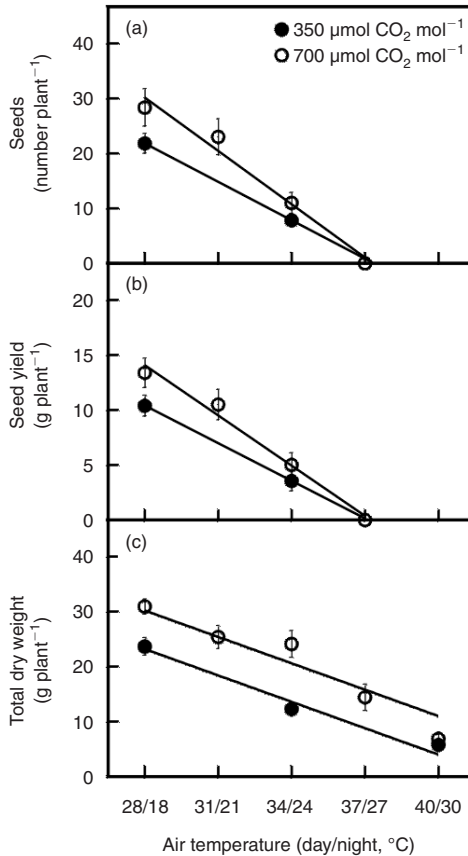
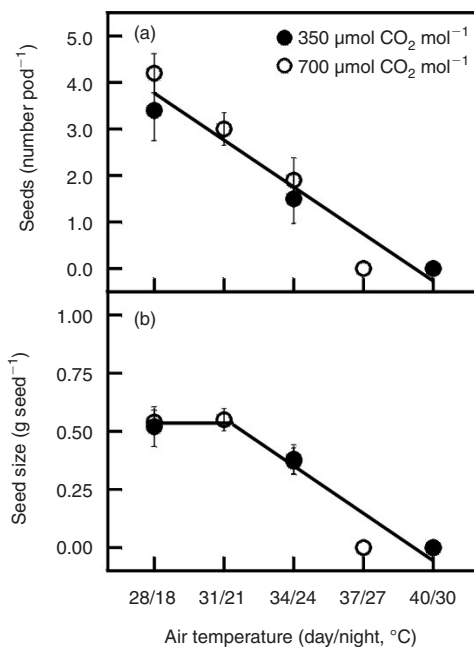


FIGURE 6. Relations between temperature and (a) number of seeds per plant, (b) seed yield per plant, and (c) total dry weight per plant of dry bean plants grown at ambient and elevated $[\text{CO}_2]$. Fitted regressions for sloping lines: (a) ambient $[\text{CO}_2]$, $Y = 87.2 - 2.3X$, $r^2 = 0.99$; elevated $[\text{CO}_2]$, $Y = 120.7 - 3.2X$, $r^2 = 0.88$; (b) ambient $[\text{CO}_2]$, $Y = 42.5 - 1.2X$, $r^2 = 0.99$; elevated $[\text{CO}_2]$, $Y = 56.7 - 1.5X$, $r^2 = 0.88$; and (c) ambient $[\text{CO}_2]$, $Y = 68.3 - 1.6X$, $r^2 = 0.95$; elevated $[\text{CO}_2]$, $Y = 75.5 - 1.6X$, $r^2 = 0.88$. (Adapted from Prasad et al., 2002.)



Thus, elevated $[\text{CO}_2]$ increases seed yield of soybean, dry bean, peanut and cowpea under optimum temperature with no nutrient deficiency and water deficit. Greater seed yields under CO_2 enrichment were attributed to increases in seed numbers due to increased branching, but not due to increases in individual seed weight or number of seeds per pod.

FIGURE 7. Relations between temperature and (a) number of seeds per pod and (b) weight per seed (seed size) at maturity, of dry bean plants grown at ambient and elevated $[\text{CO}_2]$ in dry bean. Fitted regression: (a) $Y = 13.2 - 3.4X$, $r^2 = 0.94$; and (b) $Y = 2.66 - 0.67X$, $r^2 = 0.86$. (Adapted from Prasad et al., 2002.)



Seed Quality

Three important aspects of seed quality include: (i) individual seed size; (ii) composition or nutritional quality of seed; and (iii) ability of seed to germinate and grow. Although several studies have documented the effects of elevated $[\text{CO}_2]$ on seed size, very few have examined composition, nutritional quality and germination of seeds produced at high $[\text{CO}_2]$. Despite the importance of seed composition for human and animal nutrition, research on seed quality aspects are however, limited (Murray, 1997).

Elevated $[\text{CO}_2]$ did not influence seed size in soybean (Baker et al., 1989; Pan, 1996; Thomas, 2001) and dry bean (Prasad et al., 2002). As for seed composition, Allen et al. (1988) reported no effect of elevated $[\text{CO}_2]$ on total seed N concentration in plants dependent on symbiotic N fixation. Rogers et al. (1984) reported that seed protein as a percentage of seed dry weight decreased as $[\text{CO}_2]$ increased from 331 to 910 $\mu\text{mol mol}^{-1}$, although total seed protein

per plant increased. Since Rogers et al. (1984) research was conducted in open-top field chambers; it is unlikely that the decline in seed protein was caused by constraints to the root system.

Thomas et al. (2003) studied effects of elevated $[\text{CO}_2]$ on composition of mature soybean seed at different temperature regimes and concluded that there was no effect of elevated $[\text{CO}_2]$ ($700 \mu\text{mol mol}^{-1}$) on N, P, starch, total oil, fatty acids, and total nonstructural carbohydrates compared to ambient $[\text{CO}_2]$ across all temperatures ranging from 28/18 through 44/34°C. There were no effects of elevated $[\text{CO}_2]$ (700 and $1,400 \mu\text{mol mol}^{-1}$) on nutrient composition and mineral nutrient in peanut kernels (Wu et al., 1997). Effects of elevated $[\text{CO}_2]$ on composition and nutritional quality of dry bean and cowpea are known. These crop species could respond differently than soybean and peanut because of their variable ability to fix atmospheric nitrogen, especially dry bean, which is less efficient in nitrogen fixation.

Idso and Idso (2001) reviewed effects of $[\text{CO}_2]$ on plant constituents related to animal and human health, and argued that although elevated $[\text{CO}_2]$ decreased nitrogen and protein concentration in some species, these decreases were not observed when plants were supplied with sufficient N. Decreases in mineral concentration were reported in dry bean (Porter and Grodzinski, 1984). Recently, Jablonski et al. (2002) conducted meta analysis of 79 crops species including legumes, non-legumes, C_3 and C_4 species and concluded that seed N concentration was unaffected by growth at high $[\text{CO}_2]$ (500 to $800 \mu\text{mol mol}^{-1}$) in legumes, while in non legume C_3 plants it was reduced by 15%. Legumes growing symbiotically with *Rhizobium* have an enhanced root system (Finn and Brun, 1982; Bottomely and Rogers, 1993) and may be able to support the increased N_2 fixation necessary to maintain the N concentration for an increased number of seeds per plant under elevated $[\text{CO}_2]$ (Murray, 1995). Similarly, Allen and Boote (2000) opined that legumes are often able to use increased carbon gain under elevated $[\text{CO}_2]$ for increased N_2 fixation and thus may be able to increase seed number and/or mass without a loss in seed N.

INTERACTION EFFECTS OF $[\text{CO}_2]$ AND TEMPERATURE

To properly quantify the effects of potential climate change on crops, studies on interactions of $[\text{CO}_2]$ and temperature are more important than effects of $[\text{CO}_2]$ alone, because in the future climate both of these factors are likely to increase. Therefore, in this section the interaction effect of $[\text{CO}_2]$ and temperature on carbon and water use, phenology, growth, carbohydrate accumulation, yield components, yield, and seed quality is discussed.

Carbon and Water Use Efficiency

Photosynthesis

Elevated CO₂ enhancements of leaf photosynthesis increased in a linear manner by 32 to 95% with increasing growth temperatures from 28/22 to 40/30°C (Figure 2; Vu et al., 1997). Furthermore, it was observed that at ambient [CO₂], photosynthetic rates of soybean decreased above 32/22°C, while at elevated [CO₂] photosynthetic rates at 32/22 and 36/26°C were similar and a further increase in temperature to 40/30°C decreased leaf photosynthetic rates. This clearly suggests a greater and wider temperature optima for photosynthesis of plants grown at elevated [CO₂]. Similar responses were observed for cotton (Reddy et al., 1998) and in the mechanistic model predictions by Long (1991), where the temperature optimum for light saturated photosynthesis increased by 5°C with increases in [CO₂] from 350 to 700 $\mu\text{mol mol}^{-1}$.

There was no effect of elevated [CO₂] and/or temperature up to 40/30°C on midday total Rubisco activity or protein concentration, but both elevated temperature and [CO₂] decreased initial Rubisco activities and Rubisco activation (Vu et al., 1997). A further increase in temperature to 44/34 or 48/38°C significantly decreased midday Rubisco activity and Rubisco protein concentration (Vu et al., 2001).

Interaction studies on dry bean showed negative effects of temperature on CO₂ enhancement of leaf photosynthesis (Prasad et al., 2002). For example, CO₂ enrichment increased leaf photosynthetic rate by 66, 43, and 39% at temperature regimes of 28/18, 34/24, and 40/30°C, respectively (Figure 2). Two main reasons for a greater response of soybean photosynthesis at high temperature, as suggested by Morrison and Lawlor (1999) include (i) a decreased ratio of photosynthesis to photorespiration; and (ii) a decreased ratio of gross photosynthesis to dark respiration in warmer conditions. As discussed earlier, an increase in [CO₂] decreases oxygenase activity of Rubisco and the loss of carbon through photorespiration. On the other hand, increasing temperature would increase photorespiration by lowering solubility of [CO₂] compared to O₂ and decreasing specificity of Rubisco at higher temperature. Thus, the largest effect of increased [CO₂] on photosynthetic carbon fixation is observed at high temperature (Lawlor and Keys, 1993). However, this phenomenon is not observed in all C₃ species, for example in dry bean the percentage increase in photosynthesis was greater at 28/18°C compared to that at 40/30°C (Prasad et al., 2002), while in rice, percentage enhancement was not altered over a range of temperatures between 32/23 and 38/29°C (Vu et al., 1997). These species differences could partially be attributed to different temperature optima for photosynthesis and differential effects of temperature and [CO₂] on Rubisco (Sage et al., 1989; Long, 1991; Vu et al., 1997; Bunce, 1998).

Respiration

Bunce and Ziska (1996) studied the response of three soybean cultivars from three different maturity groups at three different temperatures (20/15, 25/20, and 31/26°C) and [CO₂] (370, 555 and 740 μmol mol⁻¹) and reported that at all temperatures, growth at elevated [CO₂] decreased total respiration when measured at the growth concentration. Growth respiration as estimated from elemental composition was not affected by [CO₂] at any temperature, but increased with temperature. Pan (1996) measured soybean respiration at five temperatures (28/18, 32/22, 36/26, 40/30, and 44/34°C) at elevated [CO₂] (700 μmol mol⁻¹) and at two temperatures (28/18, and 40/30°C) at ambient [CO₂] (350 μmol mol⁻¹). He reported no interaction between [CO₂] and temperature. Plants grown and measured at higher temperature had higher specific respiration rate, regardless of [CO₂].

Stomatal Conductance, Transpiration, and Water Use Efficiency

Studies on combined effects of elevated [CO₂] and temperature on water use are scarce. High [CO₂] decreases stomatal conductance, while high temperature increases stomatal conductivity and transpiration due an increased vapor pressure gradient between leaf surface and atmosphere. Therefore, a combination of elevated [CO₂] and temperature could give variable effects. Transpiration of soybean plants increased by about 4% per °C increase in temperature in the range of 28/23 to 35/23°C (Jones et al., 1985c). They also found that photosynthetic WUE of soybean plants was decreased at high temperature due to increased transpiration caused by greater evaporative demand. Similar observations were made in peanut canopies (Stronach et al., 1994).

Pan (1996) studied the interaction effects of high [CO₂] and temperature on soybean crop water use and concluded that the extent of decreases in evapotranspiration by elevated [CO₂] were offset by elevated temperature (>36°C). Thus, more water would be needed at high temperatures. These results confirm the earlier suggestion that both increased leaf area and increased foliage temperature at doubled [CO₂] can offset reductions in crop transpiration caused by elevated [CO₂] (Allen et al., 1985). Increased WUE due to decreased stomatal conductance at high [CO₂] were offset by increased temperature (Jones et al., 1985c; Allen et al., 1985; Allen, 1999). Polley (2002) concluded that yield benefits of improved water use efficiency at high [CO₂] are eroded due to decreased harvest index at high temperatures. Therefore, if global temperatures rise with increasing [CO₂], future crop water use will increase especially in arid subtropical and tropical regions where air temperatures are already high.

Phenology, Growth, Yield, and Seed Quality

Phenology

Studies have shown that both increasing temperature and increasing $[\text{CO}_2]$ decreased the plastochron interval of soybean (Baker et al., 1989). However, the effects of temperature on phenology and development are much more prominent than those of $[\text{CO}_2]$. Temperature is the main environmental factor affecting phenology apart from photoperiod. Plants require a certain amount of heat units (thermal time) to reach each physiological development stage. At warmer temperatures, plants achieve these requirements earlier, thus enhancing physiological development in most plants. Increase in temperature within the optimal range shortens time to flowering in soybean (Baker et al., 1989), dry bean (Prasad et al., 2002), peanut (Bell et al., 1991; Awal and Ikeda, 2002), and cowpea (Craufurd et al., 1996). Long-term exposure to elevated $[\text{CO}_2]$ in soybean (Valle et al., 1985b) and dry bean (Prasad et al., 2002) increased tissue (leaf) temperature by about 2°C compared to those at ambient $[\text{CO}_2]$ at temperatures ranging from 28/18 to 40/30°C. This was mainly due to decreased transpirational cooling caused by partial stomatal closure. These increases in tissue temperature may explain the hastening of time to flowering in soybean grown at elevated $[\text{CO}_2]$ as reported by Sionit et al. (1987a, b), Allen et al. (1988), and Baker et al. (1989). Exposure to excessively high temperature delayed time to seed initiation in soybean at ambient or elevated $[\text{CO}_2]$ (Pan, 1996) and heat susceptible peanut genotype grown under ambient $[\text{CO}_2]$ (Wheeler et al., 1997).

Organ Growth and Partitioning

Although the effects of elevated $[\text{CO}_2]$ and temperature are well documented, few studies have focused on interaction between elevated $[\text{CO}_2]$ and temperature (Sionit et al., 1987a and b; Baker et al., 1989; Ahmed et al., 1993; Clifford et al., 2000; Prasad et al., 2002). Sionit et al. (1987a) studied the effects of three temperatures (18/12, 22/16, and 26/20°C) at three $[\text{CO}_2]$'s (350, 675, and 1000 $\mu\text{mol mol}^{-1}$) on growth and dry matter production of soybean. They reported that increasing $[\text{CO}_2]$ and temperature increased stem height, number of nodes, number of branches, number of leaves, leaf weight, stem weight and root weight and leaf area per plant. Similarly, increases in temperature from 26/19 to 36/29°C increased above ground dry matter and leaf area at both ambient and elevated $[\text{CO}_2]$ (Baker et al., 1989). Studies of Sionit et al. (1987a, b) were at the cool end of optimum temperature range, while those of Baker et al. (1989) were slightly higher in the optimum range. Pan (1996) studied the effects of elevated $[\text{CO}_2]$ at optimal and super-optimal tempera-

tures (28/18, 32/22, 36/26, 40/30, and 44/34°C). It was observed that the optimum temperature for leaf area growth during the vegetative phase was 36/26°C, whereas lower or higher temperature decreased leaf area growth. At later stages, leaf area of plants grown at 44/34°C was greater than other treatments; this was because flowering and pod formation were delayed and decreased at high temperatures and available assimilates were used for continued leaf growth. There were no interactions between temperatures and $[\text{CO}_2]$, and doubling of $[\text{CO}_2]$ increased total dry matter at all temperatures. Elevated temperature increased dry matter partitioning to stems and leaves, while doubling of $[\text{CO}_2]$ decreased partitioning to leaves and pods, and increased dry matter partitioning to stems.

In dry bean, Prasad et al. (2002) reported no interaction between elevated $[\text{CO}_2]$ and temperatures on dry matter production and seed yield. As temperature increased from 28/18 to 40/30°C, total dry matter production decreased linearly by $1.6 \text{ g plant}^{-1} \text{ } ^\circ\text{C}^{-1}$ at both ambient and elevated $[\text{CO}_2]$ (Figure 6).

Root Growth and Nitrogen Fixation

Interaction effects of elevated $[\text{CO}_2]$ and temperature on root growth and nodule function of grain legumes have not been well studied. Separate studies have shown a significant influence of elevated $[\text{CO}_2]$ (Rogers et al., 1992; Hardy and Havelka 1975) or soil and/or air temperature (Prasad et al., 2000) on root growth and nodule dry weights. As mentioned earlier, elevated $[\text{CO}_2]$ increased root growth mass, growth and distribution in soybean. Conversely, high soil temperature significantly decreased root to shoot ratio, root growth, nodule weight and nodule numbers in peanut (Prasad et al., 2000, 2001a). Furthermore, it was noticed that decreases in number of nodules and nodule dry weights were more sensitive to high soil temperature than high air temperature (Prasad et al., 2001b). Various aspects of rhizobium-legume symbiosis are known to be affected by high soil temperatures including growth and survival of rhizobia, formation of root hairs, formation of infection threads, structural development of root nodules, and activity of nitrogenase enzyme, resulting in reduced nodule numbers, and nodule mass per plant (Giller and Willson, 1991). However, it is not known if deleterious effects of high temperature on root growth and nodule function could be overcome by elevated $[\text{CO}_2]$.

Serraj et al. (1998) studied the combined effects of elevated $[\text{CO}_2]$ and drought on nodulation and N_2 fixation of soybean. They concluded that under drought conditions, elevated $[\text{CO}_2]$ delayed decreases in N_2 fixation rates associated with drying. Elevated $[\text{CO}_2]$ also allowed the plants under drought to sustain significant increases in nodule number and mass relative to those under ambient $[\text{CO}_2]$. Thus, it is possible that future increases in $[\text{CO}_2]$ will benefit soybean production by increasing the drought tolerance of N_2 fixation,

increasing carbon assimilation, and reducing water requirement. Similar interaction studies with $[\text{CO}_2]$ and elevated temperature need further attention.

Carbohydrate Accumulation

Carbohydrate metabolism in soybean leaves grown at elevated $[\text{CO}_2]$ remained relatively high compared to leaves grown at ambient $[\text{CO}_2]$ at temperatures ranging between 28/18 and 44/34°C (Vu et al., 2001). However, as temperature increased from 28/18 to 44/34°C, predawn and midday starch were decreased at both ambient and elevated $[\text{CO}_2]$. The net increase in starch and sugar accumulation (i.e., difference between predawn and midday values) was highest at 40/30°C, and decreased with a further increase or decrease in temperature to 28/18 or 48/38°C. Similarly the midday activity of Rubisco was decreased at temperatures above 32/23°C in both ambient and elevated $[\text{CO}_2]$ (Vu et al., 1997). It was observed that even at a growth temperature of 44/34°C, photosynthesis and carbohydrate metabolism under elevated $[\text{CO}_2]$ were greater than those grown at 28/18°C under ambient $[\text{CO}_2]$ (Vu et al., 1997, 2001). They concluded that soybean carbohydrate metabolism and photosynthesis would not be hindered by predicted changes in elevated $[\text{CO}_2]$ and/or temperatures.

Yield and Yield Components

Beneficial effects of elevated $[\text{CO}_2]$ on photosynthesis, carbohydrate metabolism and vegetative growth are not always reflected in seed yields, because vegetative and reproductive processes have different responses to temperature and therefore show different stimulations by $[\text{CO}_2]$ at elevated temperatures (Boote et al., 1997). In addition, reproductive development is more sensitive to high temperatures than overall plant biomass production, vegetative processes or photosynthesis. Temperatures that stimulate photosynthesis and vegetative growth are often detrimental to reproductive growth, resulting in lower yield. Lower seed yields at super-optimal temperatures are due mainly to a decreased number of fruits and a smaller seed size (Baker et al., 1989; Pan, 1996; Prasad et al., 2002). Lower fruit numbers at super-optimal temperatures are caused by decreased fruit-set, due mainly to decreased pollen production and poor pollen viability (Hall, 1992; Gross and Kigel, 1994; Prasad et al., 1999, 2000, 2002).

There were no interactions between temperature and $[\text{CO}_2]$ on seed yields or harvest index. Seed yields of soybean were decreased at temperature >36/26°C, due to lower seed numbers per plant, lower numbers of seed per pod and smaller seed size (Pan, 1996; Thomas, 2001). Harvest index of soybean progressively decreased with increasing day temperature from 28/18 to 36/26°C

in both elevated and ambient $[\text{CO}_2]$ (Baker et al., 1989). Similarly, Prasad et al. (2002) reported no interaction effect between $[\text{CO}_2]$ and temperature on seed-set in dry bean. As temperature increased from 28/18 to 40/30°C, seed-set was reduced by 6% per °C rise in temperature at both ambient and elevated $[\text{CO}_2]$ (Figure 5). Furthermore, the fact that the ceiling temperature for seed set was 2°C lower at elevated $[\text{CO}_2]$ suggests that yield losses associated with high temperature will increase with elevated $[\text{CO}_2]$. Similar effects were observed in rice (Matsui et al., 1997), where the critical temperature for pollen fertility was lower by 1.5 to 2°C in plants grown at elevated $[\text{CO}_2]$ compared to those at ambient $[\text{CO}_2]$. Seed yields of rice decreased 10% per °C rise at temperatures from 26 to 36°C under both ambient and elevated $[\text{CO}_2]$ (Baker and Allen, 1993). Both short-term and long-term exposure to super-optimal temperature decreased seed yields of soybean and peanut (Wheeler et al., 2000). Similar yield decreases due to super-optimal temperature were observed in several other crops (Reddy and Hodges, 2000). Exposure to temperatures > 28/18°C decreased seed number, seed yield per plant, number of seeds per pod, and seed size of dry bean at both ambient and elevated $[\text{CO}_2]$ (Figures 6 and 7; Prasad et al., 2002).

Clearly, there are no beneficial interactions of $[\text{CO}_2]$ at higher temperatures and damage caused by high temperature on reproductive growth and seed yield of soybean (Baker et al., 1989; Pan 1996; Ferris et al., 1999; Wheeler et al., 2000; Thomas, 2001), dry bean (Prasad et al., 2002), and cowpea (Hall, 1992) were not overcome by elevated $[\text{CO}_2]$. It is therefore concluded that greater $[\text{CO}_2]$ enhancements with increasing temperature for photosynthesis and vegetative dry matter production are not applicable for reproductive growth, yield components, and seed yield.

The optimum temperature for seed yield and harvest index of soybean (Pan, 1996), peanut (Hammer et al., 1995) and cowpea is close to 25°C and even lower for dry bean (Prasad et al., 2002). Average temperatures of 25°C are very common in subtropical and tropical regions where these crops are currently grown. For example, mean air temperatures in Florida are about 26°C in the normal summer season, with up to 27°C in hot summers (Boote et al., 1997). Therefore, any warming of climate will decrease seed yields of these crops in regions where present temperatures are close to optimum irrespective of changes in $[\text{CO}_2]$. However in regions where temperatures are cool seed yield would be benefited by small increases in temperatures as long as they do not exceed optimum temperatures.

Seed Quality

There were no effects of $[\text{CO}_2]$ or interaction between $[\text{CO}_2]$ and temperature on seed size and percent shriveled seeds in soybean (Pan, 1996; Thomas,

2001). Increase in growth temperature from 28/18 to 40/30°C decreased seed size and increased the percentage of shriveled seed under both ambient and elevated $[\text{CO}_2]$. In a similar study on dry bean, Prasad et al. (2002) reported that seed size was significantly decreased with an increase in temperature above 31/21°C at both ambient and elevated $[\text{CO}_2]$. There was no effect of elevated $[\text{CO}_2]$ or interaction between $[\text{CO}_2]$ and temperature on number of seeds per pod and seed size (Figure 7).

Seed composition and transcript abundance were significantly affected by temperature, but not by $[\text{CO}_2]$ or interaction of $[\text{CO}_2]$ and temperature (Thomas et al., 2003). It was reported that oil concentration increased with increasing temperature with an optimum at 25 to 28°C, above which the oil concentration declined (Dornbos and Mullen, 1992; Gibson and Mullen, 1996a; Piper and Boote, 1999). In contrast, seed protein concentration of soybean was constant or slightly increased at temperatures between 16 and 25°C, but increased at temperatures above 25°C (Wolf et al., 1982; Dornbos and Mullen, 1992; Gibson and Mullen, 1996a; Piper and Boote, 1999).

Studies on soybean have shown that seeds obtained from plants grown at high day (35°C) and high night (30°C) temperatures had reduced subsequent seed germination and seedling vigor (Gibson and Mullen, 1996b). The extent of reductions in seed germination and vigor by high temperature was influenced by duration of temperature and the phase of reproductive growth. Greater reductions were observed with longer duration of exposure to high temperatures especially during seed fill and maturation. However, further research is required across other cultivars and crop species to clearly understand effects of super-optimal temperature and elevated $[\text{CO}_2]$ on seed quality.

RESPONSE OF CULTIVARS TO $[\text{CO}_2]$ AND/OR TEMPERATURE

Cultivars within the same crop species are reported to differ in their responses to $[\text{CO}_2]$ and temperature and their interactions. Ziska et al. (2001) tested nine soybean cultivars differing in determinacy, maturity group and morphology in response to elevated $[\text{CO}_2]$. They found that although all cultivars showed a significant increase in seed yield with elevated $[\text{CO}_2]$ (approximately 40%), Mandarin, an ancestral indeterminate cultivar, showed a greater relative response of seed yield to elevated $[\text{CO}_2]$ (approximately 80%). The greater response of Mandarin was not related to any vegetative parameters, but to a greater pod weight per plant and seed weight from branches.

Ahmed et al. (1993) studied the response of three cowpea cultivars with varying heat tolerance to high night temperatures under ambient and elevated $[\text{CO}_2]$ (Table 7). Results showed that under high night temperatures (30°C), the heat sensitive cultivars did not produce any flowers (cv. CB 5) and pods

TABLE 7. Reproductive responses of contrasting cowpea lines grown at two $[\text{CO}_2]$ concentrations and two day/night temperature regimes. Values are means \pm SEM. (Adapted from Ahmed et al., 1993.)

Genotype	Temperature (day/night, °C)	Carbon dioxide concentration (μmol mol ⁻¹)						Total shoot biomass (g plant ⁻¹)		
		350		700		350			700	
		Period to first flower (d)		Flowers (no. plant ⁻¹)		Pods (no. plant ⁻¹)				
CB 5	33/20	30.3 ± 0.3	30.8 ± 0.3	74 ± 6	84 ± 12	15 ± 1	26 ± 2	91 ± 3	109 ± 5	
	33/30	++	++	0	0	-	-	76 ± 5	82 ± 10	
7964	33/20	29.5 ± 0.3	30.3 ± 0.3	65 ± 6	64 ± 2	23 ± 2	27 ± 2	66 ± 3	89 ± 4	
	33/30	24.8 ± 0.3	25.3 ± 0.2	100 ± 8	104 ± 8	0	0	58 ± 7	63 ± 3	
518	33/20	30.5 ± 0.3	30.3 ± 0.3	70 ± 4	81 ± 12	28 ± 1	42 ± 5	89 ± 4	118 ± 5	
	33/30	24.5 ± 0.3	25.6 ± 0.2	75 ± 3	70 ± 4	28 ± 1	40 ± 2	91 ± 5	103 ± 5	

++: Did not flower during the experiment which lasted 6 weeks.

(cv. 7964) under both ambient and elevated $[\text{CO}_2]$. In contrast, the heat tolerant cultivar (cv. 518) produced a greater number of pods and a higher pod yield under high temperatures and responded strongly to CO_2 enrichment at high temperatures. Increased pod numbers in the heat tolerant cultivar were a result of greater fruit-set.

Cultivars of soybean (Sapra and Anaele, 1991; Srinivasan et al., 1996), peanut (Ntare et al., 2001; Craufurd et al., 2002, 2003; Kakani et al., 2002), dry bean (Agtunong et al., 1992), and cowpea (Ahmed et al., 1993; Ehlers and Hall, 1996) are known to vary in their response to high temperatures. However, further research is necessary to test if heat tolerant cultivars of legumes and other seed producing crops are more or less responsive to elevated $[\text{CO}_2]$.

Cultivars with heat tolerance during reproductive development, high harvest index, high photosynthetic capacity per unit leaf area, small leaves and low leaf area per unit ground area, under present levels of $[\text{CO}_2]$ will be most responsive to both high and intermediate temperatures (Hall and Allen, 1993). Therefore, research should be focused on searching for cultivars that show these characters and testing them under controlled and field environments. In addition, farmers may also make adjustments in planting dates, selection of crop, and selection of cultivars, so as to avoid severe yield losses. Future research should focus on designing suitable crop management practices for future climates, which will not only have higher $[\text{CO}_2]$ and mean temperatures, but also more short episodes of extreme temperature events.

CONCLUSIONS

Photosynthetic rates of soybean, dry bean, peanut, and cowpea were enhanced when grown at high $[\text{CO}_2]$; however, the extent of stimulation varied with temperature. There were species differences in these responses, with soybean responding positively and dry bean responding negatively at higher temperatures. Decreases in stomatal conductivity and transpiration caused by partial stomatal closure under elevated $[\text{CO}_2]$ were more than offset by increased leaf area and vapor pressure deficits caused by increased leaf temperature. These changes in energy balance of leaves resulted in similar total water use by crop canopies when expressed on a land area basis. There was very little or no effect of elevated $[\text{CO}_2]$ on major phenostages such as flowering of these legumes, which were driven mainly by temperature and photoperiod. Elevated $[\text{CO}_2]$ increased total biomass production due to larger total leaf area, greater stem growth, and greater root growth. Seed yields increased at elevated $[\text{CO}_2]$ under optimal temperature and irrigated conditions due to greater numbers of pods and seeds caused by increased branching. However, at super-optimal temperature, fruit-set, number of seeds, seed growth rates, individual seed

weight, and harvest index decreased under both ambient and elevated $[\text{CO}_2]$. Adverse effects of super-optimal temperature on seed yield and yield components were not offset by stimulation of photosynthesis or growth under elevated $[\text{CO}_2]$. In the future, if increases in $[\text{CO}_2]$ are associated with increases in temperature, seed yield will decrease in regions where present temperatures are already close to optimum. Future research should be aimed at identifying heat tolerant cultivars that can produce more seeds, sustain them to maturity, and utilize available carbohydrates more efficiently to improve crop productivity under hostile climatic conditions.

REFERENCES

- Acock, B. and L.H. Allen, Jr. (1985). Crop responses to elevated carbon dioxide concentration. pp 53-97. In: B.R. Strain and J.D. Cure (eds.), *Direct Effects of Increasing Carbon Dioxide on Vegetation*. DOE/ER-0238. U.S. Department of Energy, Carbon Dioxide Research Division, Washington, DC.
- Acock, B., V.R. Reddy, H.F. Hodges, D.N. Baker and J.M. McKinion (1985). Photosynthetic response of soybean canopies to full season carbon dioxide enrichment. *Agronomy Journal* 77: 942-947.
- Agtunong, T.P., R. Redden, M.A. Menggenang, C. Searle and S. Fukai. (1992). Genotypic variation in response to high-temperature at flowering in common bean (*Phaseolus vulgaris* L.). *Australian Journal of Experimental Agriculture* 32:1135-1140.
- Ahmed, F.E., A.E. Hall and M.A. Madore. (1993). Interactive effects of high-temperature and elevated carbon dioxide concentration on cowpea [*Vigna unguiculata* (L.) Walp]. *Plant Cell and Environment* 16:835-842.
- Ainsworth, E.A., P.A. Davey, C.J. Bernacchi, O.C. Dermody, E.A. Heaton, D.J. Moore, P.B. Morgan, S.L. Naidu, H.S.Y. Ra, X.G. Zhu, P.S. Curtis and S.P. Long. (2002). A meta-analysis of elevated $[\text{CO}_2]$ effects on soybean (*Glycine max*) physiology, growth and yield. *Global Change Biology* 8:695-709.
- Allen, L.H., Jr., J.T. Baker and K.J. Boote. (1996). The CO_2 fertilization effect: higher carbohydrate production and retention as biomass and seed yield. pp. 65-100. In: F. Bazzaz and W. Sombroek (eds.), *Global Climate Change and Agricultural Production*. FAO, Rome, Italy.
- Allen, L.H., Jr. (1999). Evapotranspiration responses of plant and crops to carbon dioxide and temperature. *Journal of Crop Production* 2: 37-70.
- Allen, L.H., Jr. and K.J. Boote. (2000). Crop ecosystems responses to climate change: soybean. pp. 133-160. In: K.R. Reddy and H.F. Hodges (eds.), *Climate Change and Global Crop Productivity*. CABI Publishing, Oxon, UK.
- Allen, L.H., Jr., E.C. Bisbal and K.J. Boote. (1998). Nonstructural carbohydrates of soybean plants grown in subambient and superambient levels of CO_2 . *Photosynthesis Research* 56:143-155.
- Allen, L.H., Jr., E.C. Bisbal, K.J. Boote and P.H. Jones. (1991). Soybean dry matter allocation under subambient and superambient levels of carbon dioxide. *Agronomy Journal* 83: 875-883.

- Allen, L.H., Jr., E.C. Bisbal, W.J. Campbell and K.J. Boote. (1990). Carbon dioxide effects on soybean developmental stages and expansive growth. *Soil and Crop Science Society of Florida Proceedings* 49:124-131.
- Allen, L.H., Jr., J.C.V. Vu, R.R. Valle, K.J. Boote and P.H. Jones. (1988). Non-structural carbohydrates and nitrogen of soybean grown under carbon dioxide enrichment. *Crop Science* 28: 88-94.
- Allen, L.H., Jr., P.H. Jones and J.W. Jones. (1985). Rising atmospheric CO₂ and evapotranspiration. pp. 13-17. In: *Advances in Evapotranspiration*. ASAE Publication no. 14-16. American Society of Agricultural Engineers, St. Joseph, Michigan.
- Allen, L.J., Jr. (1994). Carbon dioxide increase: direct impacts on crops and indirect effects mediated through anticipated climate changes. pp. 425-459. In: K.J. Boote, J.M. Bennett, T.R. Sinclair and G.M Paulsen (eds.), *Physiology and Determination of Crop Yield*. ASA, CSSA and SSSA, Madison, Wisconsin.
- Allen, L.H., Jr., E.C. Bisbal, W.J. Campbell and K.J. Boote. (1987). Responses of vegetation to rising CO₂: Photosynthesis, biomass and seed yield of soybean. *Global Biochemical Cycles* 1: 1-14.
- Amthor, J.S. (1991). Respiration in future, higher CO₂ world. *Plant Cell and Environment* 14: 13-20.
- Amthor, J.S. (1997). Plant respiratory responses to elevated carbon dioxide partial pressure. pp. 35-77. In: L.H. Allen, M.B. Kirkhan, D.M. Olsztik and C.E. Whitman (eds.), *Advances in Carbon Dioxide Effects Research*. ASA Special Publication No. 61, ASA-CSSA-SSSA, Madison, Wisconsin.
- Arp, W.J. (1991). Effects of source-sink relations on photosynthetic acclimation to elevated CO₂. *Plant Cell and Environment* 14:869-875.
- Awal, M.A. and T. Ikeda. (2002). Effects of changes in soil temperature on seedling emergence and phenological development in field-grown stands of peanut (*Arachis hypogaea*). *Environmental and Experimental Botany* 47: 101-113.
- Baker, J.T. and L.H. Allen, Jr. (1993). Contrasting crop species responses to CO₂ and temperature-rice, soybean and citrus. *Vegetatio* 104:239-260.
- Baker, J.T., L.H. Allen, Jr., K.J. Boote, P. Jones and J.W. Jones. (1989). Response of soybean to air temperature and carbon dioxide concentration. *Crop Science* 29: 98-105.
- Bell, M.J., R. Shorter and R. Mayer. (1991). Cultivar and environmental effects on growth and development of peanut (*Arachis hypogaea* L.). 1. Emergence to flowering. *Field Crops Research* 27: 17-33.
- Bhattacharya, N.C., S. Bhattacharya, P.K. Biswas and B.R. Strain. (1987). Partitioning of photoassimilates into carbohydrates and proteins of cowpea (*Vigna unguiculata* L.) to CO₂ enrichment environment during different stages of vegetative and reproductive growth. *Hortscience* 22:1113-1113.
- Bhattacharya, S., N.C. Bhattacharya, P.K. Biswas and B.R. Strain. (1985). Response of cow pea (*Vigna unguiculata* L.) to CO₂ enrichment environment on growth, dry matter production and yield components at different stages of vegetative and reproductive growth. *Journal of Agricultural Sciences* (Cambridge) 105:527-534.
- Biswas, P.K. and D.R. Hileman. (1985). *Response of Vegetation to Carbon Dioxide: Field Studies of Sweet Potato and Cowpea in Response to Elevated Carbon Diox-*

- ide*. Report 022, U.S. Department of Energy, Carbon Dioxide Research Division, Office of Energy Research, Washington, DC.
- Boote, K.J., N.B. Pickering and L.H. Allen, Jr. (1997). Plant modeling: advances and gaps in our capability to predict future crop growth and yield. pp. 179-228. In: L.H. Allen, Jr., M.B. Kirkhan, D.M. Olsztik and C.E. Whitman (eds.). *Advances in Carbon Dioxide Effects Research*. ASA Special Publication No. 61, ASA-CSSA-SSSA, Madison, Wisconsin.
- Bottomley, P.A. and H.H. Rogers. (1993). NMR imaging of root water distribution in intact *Vicia faba* L. plants in elevated atmospheric CO₂. *Plant Cell and Environment* 16: 335-338.
- Bowes G. (1996) Photosynthetic responses to changing atmospheric carbon dioxide. pp. 387-407. In: N.R. Baker (ed.). *Photosynthesis and the Environment. Advances in Photosynthesis* Vol. 5, Kluwer, Dordrecht.
- Bunce, J.A. (1998). The temperature dependence of the stimulation of photosynthesis by elevated carbon dioxide in wheat and barley. *Journal of Experimental Botany* 49:1555-1561.
- Bunce, J.A. and F. Caulfield. (1991). Reduced respiratory carbon dioxide efflux during growth at elevated carbon dioxide in 3 herbaceous perennial species. *Annals of Botany* 67: 325-330.
- Bunce, J.A. and L.H. Ziska. (1996). Responses of respiration to increases in carbon dioxide concentration and temperature in three soybean cultivars. *Annals of Botany* 77:507-514.
- Campbell, W.J., L.H. Allen, Jr. and G. Bowes. (1988). Effects of CO₂ Concentration on rubisco activity, amount, and photosynthesis in soybean leaves. *Plant Physiology* 88:1310-1316.
- Campbell, W.J., L.H. Allen, Jr. and G. Bowes. (1990). Response of soybean canopy photosynthesis to CO₂ concentration, light, and temperature. *Journal of Experimental Botany* 41:427-433.
- Chen, J.J. and J.M. Sung. (1990). Gas exchange rate and yield responses of Virginia type peanut to carbon dioxide enrichment. *Crop Science* 30:1085-1089.
- Chen, X.M., G.B. Begonia, D.M. Alm and J.D. Hesketh. (1995). Sooybean stomatal acclimation to long-term exposure to CO₂-enriched atmospheres. *Photosynthetica* 31: 51-57.
- Clifford, S.C., C.R. Black, J.A. Roberts, I.M. Stronach, P.R. Singletonjones, A.D. Mohamed and S.N. Azamali. (1995). The effect of elevated atmospheric CO₂ and drought on stomatal frequency in groundnut (*Arachis hypogaea* L.). *Journal of Experimental Botany* 46:847-852.
- Clifford, S.C., I.M. Stronach, A.D. Mohamed, S.N. Azamali and N.M.J. Crout. (1993). The effects of elevated atmospheric carbon dioxide and water stress on light interception, dry matter production and yield in stands of groundnut (*Arachis hypogaea* L.). *Journal of Experimental Botany* 44:1763-1770.
- Clifford, S.C., I.M. Stronach, C.R. Black, P.R. Singleton-Jones, S.N. Azam-Ali and N.M.J. Crout. (2000). Effects of elevated CO₂, drought and temperature on the water relations and gas exchange of groundnut (*Arachis hypogaea*) stands grown in controlled environment glasshouses. *Physiologia Plantarum* 110:78-88.

- Coleman, J.S., K.D.M. McConnaughay and F.A. Bazzaz. (1993). Elevated CO₂ and plant nitrogen use—is reduced tissue nitrogen concentration size dependent. *Oecologia* 93: 195-200.
- Cowling, S.A. and R.F. Sage. (1998). Interactive effects of low atmospheric CO₂ and elevated temperature on growth, photosynthesis and respiration in *Phaseolus vulgaris*. *Plant Cell and Environment* 21: 427-435.
- Craufurd, P.Q., E.H. Roberts, R.H. Ellis and R.J. Summerfield. (1996). A stability analysis of time to flowering as a screen for responsiveness to temperature and photoperiod in cowpea (*Vigna unguiculata*). *Euphytica* 88: 77-84.
- Craufurd, P.Q., P.V.V. Prasad and R.J. Summerfield. (2002). Dry matter production and harvest index at high temperature in peanut. *Crop Science* 42: 146-151.
- Craufurd, P.Q., P.V.V. Prasad, V.G. Kakani, T.R. Wheeler and S.N. Nigam. (2003). Heat tolerance in peanut. *Field Crops Research* 80: 63-77.
- Cure, J.D. (1985). Carbon dioxide doubling response: a crop survey. pp 99-116. In: B.R. Strain and J.D. Cure (eds.). *Direct Effects of Increasing Carbon Dioxide on Vegetation*. DOE/ER-0238. U.S. Department of Energy, Carbon Dioxide Research Division, Washington, DC.
- Cure, J.D. and B. Acock. (1986). Crop responses to carbon dioxide doubling: a literature survey. *Agricultural and Forest Meteorology* 38: 127-145.
- Cure, J.D., T.W. Rufty and D.W. Israel. (1988). Phosphorus stress effects on growth and seed yield responses of nonnodulating soybean to elevated carbon dioxide. *Agronomy Journal* 80: 897-902.
- Davis, W.J., T.A. Mansfield and A.M. Hetherington. (1990). Sensing of soil water status and the regulation of plant growth and development. *Plant Cell and Environment* 13: 709-719.
- Dornbos, D.L. and R.E. Mullen. (1992). Soybean seed protein and oil content and fatty-acid composition adjustments by drought and temperature. *Journal of the American Oil Chemists Society* 69: 228-231.
- Drake, B.G., J. Azcon-Bieto, J. Berry, J. Bunce, P. Dijkstra, J. Farrar, R.M. Gifford, M.A. Gonzalez-Meler, G. Koch, H. Lambers, J. Siedow and S. Wullschlegel. (1999). Does elevated atmospheric CO₂ concentration inhibit mitochondrial respiration in green plants? *Plant Cell and Environment* 22: 649-657.
- Ehlers, J.D. and A.E. Hall. (1996). Genotypic classification of cowpea based on responses to heat and photoperiod. *Crop Science* 36: 673-679.
- Ehret, D.L. and P.A. Jolliffe. (1985). Photosynthetic carbon dioxide exchange of bean plants grown at elevated carbon dioxide concentrations. *Canadian Journal of Botany* 63:2026-2030.
- Ellis, R.H., P.Q. Craufurd, R.J. Summerfield and E.H. Roberts. (1995). Linear relations between carbon dioxide concentration and rate of development towards flowering in sorghum, cowpea and soybean. *Annals of Botany* 75: 193-198.
- FAO. (2001). *Food and Agricultural Organization: Statistical Data Base*. www.fao.org/.
- Ferris, R., T.R. Wheeler, P. Hadley and R.H. Ellis. (1998). Recovery of photosynthesis after environmental stress in soybean grown under elevated CO₂. *Crop Science* 38:948-955.

- Ferris, R., T.R. Wheeler, R.H. Ellis and P. Hadley. (1999). Seed yield after environmental stress in soybean grown under elevated CO₂. *Crop Science* 39: 710-718.
- Finn, G.A. and W.A. Brun. (1982). Effects of atmospheric CO₂ enrichment on growth, nonstructural carbohydrate content and root nodule activity in soybean. *Plant Physiology* 69: 327-331.
- Gibson, L.R. and R.E. Mullen. (1996a). Soybean seed composition under high day and night temperatures. *Journal of the American Oil Chemists Society* 73: 733-737.
- Gibson, L.R. and R.E. Mullen. (1996b). Soybean seed quality reductions by high day and night temperature. *Crop Science* 36: 1615-1619.
- Gifford, R.M., H. Lambers and J.I.L. Morrison. (1985). Respiration of crop species under CO₂ enrichment. *Physiologia Plantarum* 63: 351-356.
- Giller, K.E. and K.J. Wilson (1991). *Nitrogen Fixation in Tropical Cropping Systems*. CABI Publishing, Oxon, England, UK.
- Gross, Y. and J. Kigel. (1994). Differential sensitivity to high temperature of stages in the reproductive development of common bean (*Phaseolus vulgaris* L.). *Field Crops Research* 36: 201-212.
- Hall, A.E. (1992). Breeding for heat tolerance. *Plant Breeding Review* 10: 129-168.
- Hall, A.E. and L.H. Allen. (1993). Designing cultivars for the climatic conditions of the next century. pp. 291-297. In: D.R. Buxton et al. (eds.). *International Crop Science Congress I*, CSSA, Madison, Wisconsin, USA.
- Hammer, G.L., T.R. Sinclair, K.J. Boote, G.C. Wright, H. Meinke and M.J. Bell. (1995). A peanut simulation model: I. Model development and testing. *Agronomy Journal* 87: 1085-1093.
- Hardman, L.L. and W.A. Brun. (1971). Effects of atmospheric carbon dioxide enrichment at different developmental stages on growth and yield components of soybeans. *Crop Science* 11: 886-888.
- Hardy, R.W.F. and U.D. Havelka. (1973). Symbiotic N₂ fixation: multifold enhancement by CO₂ enrichment of field grown soybean. *Plant Physiology* 48: 35.
- Hardy, R.W.F. and U.D. Havelka. (1975). Photosynthate as a major factor limiting nitrogen fixation by field-grown legumes with emphasis on soybean. pp. 421-439. In: P.S. Nutman (ed.). *Symbiotic Nitrogen Fixation in Plant*. Cambridge University Press, London, England.
- Harlan, J.R. (1992). *Crops and Man*, 2nd edn. American Society of Agronomy and Crop Science Society of American, Madison, Wisconsin, USA.
- Hesketh, J.D., J.T. Woolley and D.B. Peters. (1984). Leaf photosynthetic CO₂ exchange-rates in light and CO₂ enriched environments. *Photosynthetica* 18: 536-540.
- Houghton J.T., Y. Ding, D.J. Griggs, M. Noguer, P.J. van der Linden and D. Xiaosu (Eds.). (2001). *Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC)*. Cambridge University Press, UK. pp. 944.
- Huber, S.C., H.H. Rogers and F.L. Mowry. (1984). Effects of water stress on photosynthesis and carbon partitioning in soybean (*Glycine max* [L.] Merr) plants grown in the field at different CO₂ levels. *Plant Physiology* 76:244-249.
- Idso, S.B. and K.E. Idso. (2001). Effects of atmospheric CO₂ enrichment on plant constituents related to animal and human health. *Environmental and Experimental Botany* 45: 179-199.

- Jablonski, L.M., X.Z. Wang and P.S. Curtis. (2002). Plant reproduction under elevated CO₂ conditions: a meta-analysis of reports on 79 crop and wild species. *New Phytologist* 156: 9-26.
- Jahnke, S. (2001). Atmospheric CO₂ concentration does not directly affect leaf respiration in bean or poplar. *Plant Cell and Environment* 24: 1139-1151.
- Jahnke, S. and M. Krewitt. (2002). Atmospheric CO₂ concentration may directly affect leaf respiration measurement in tobacco, but not respiration itself. *Plant Cell and Environment* 25: 641-651.
- Jolliffe, P.A. and D.L. Ehret. (1985). Growth of bean plants at elevated carbon dioxide concentrations. *Canadian Journal of Botany* 63: 2021-2025.
- Jones, P., J.W. Jones and L.H. Allen, Jr. (1985a). Seasonal canopy CO₂ exchange, water use, and yield components in soybean grown under different CO₂ and water stress conditions. *Transactions in American Society of Agricultural Engineers* 28: 2021-2028.
- Jones, P., J.W. Jones and L.H. Allen, Jr. (1985c). Response of soybean canopy growth, photosynthesis, and transpiration to whole-day temperature changes in different CO₂ environment. *Agronomy Journal* 77: 119-126.
- Jones, P., L.H. Allen, Jr., J.W. Jones and R. Valle. (1985b). Photosynthesis and transpiration responses of soybean canopies to short term and long term CO₂ treatments. *Agronomy Journal* 77: 119-126.
- Jones, P., L.H. Allen, Jr., J.W. Jones, K.J. Boote and W.J. Campbell. (1984). Soybean canopy growth, photosynthesis, and transpiration responses to whole season carbon dioxide enrichment. *Agronomy Journal* 76: 633-637.
- Kakani, V.G., P.V.V. Prasad, P.Q. Craufurd and T.R. Wheeler. (2002). Response of *in-vitro* pollen germination and pollen tube growth of peanut to high temperature. *Plant Cell and Environment* 25: 1651-1661.
- Kimball, B.A. (1983). Carbon dioxide and agricultural yield: an assemblage and analysis of 430 prior observations. *Agronomy Journal* 75: 779-788.
- Kimball, B.A. (1985). Adaptation of vegetation and management practices to a higher carbon dioxide world. pp. 185-204. In: B.R. Strain and J.D. Cure (eds.). *Direct Effects of Increasing Carbon Dioxide on Vegetation*. U.S. Department of Energy, DOE/ER-0238, Washington, DC.
- Kimball, B.A., J.R. Mauney, G. Guinn, F.S. Nakayama, P.J. Pinter, Jr., K.L. Clawson, S.B. Idso, G.D. Butler and J.R. Radin. (1984). *Response of Vegetation to Carbon Dioxide, Ser 023. Effect of Increasing Atmospheric CO₂ on the Yield and Water of crops*. U.S. Department of Energy and USDA. U.S. Water Conservation Laboratory and U.S. Western Cotton Research Laboratory, USDA-ARS, Phoenix, AZ.
- Lawlor, D.W. and A.J. Keys. (1993). Understanding photosynthetic adaptation to changing climate. pp. 85-106. In: L. Fowden, T.A. Mansfield and J. Stoddart (eds.). *Plant Adaptation to Environmental Stress*. Chapman and Hill, London.
- Leadley, P.W. and J.F. Reynolds. (1988). Effects of elevated carbon dioxide on estimation of leaf area and leaf dry weights of soybean. *American Journal of Botany* 75: 1771-1774.
- Long, S.P. (1991). Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO₂ concentration: has its importance been underestimated? *Plant Cell and Environment* 14: 729-739.

- Long, S.P. and J.E. Hallgren. (1993). Measurement of CO₂ assimilation by plants in the field and the laboratory. pp. 129-167. In: D.O. Hall, J.M.O. Scurlock, H.R. Bolhar-Nordenkamp, R.C. Leegood and S.P. Long (eds.). *Photosynthesis and Production in Changing Environment. A Field and Laboratory Manual*. Chapman and Hall, London.
- Lopez, F.B., T.L. Setter and C.R. McDavid. (1987). Carbon dioxide and light responses of photosynthesis in cowpea and pigeonpea during water deficit and recovery. *Plant Physiology* 85: 990-995.
- Matsui, T., O.S. Namuco, L.H. Ziska and T. Horie. (1997). Effects of high temperature and CO₂ concentration on spikelet sterility in indica rice. *Field Crops Research* 51: 213-219.
- Mjwara, J.M., C.E.J. Botha and S.E. Radloff. (1996). Photosynthesis, growth and nutrient changes in non-nodulated *Phaseolus vulgaris* grown under atmospheric and elevated carbon dioxide conditions. *Physiologia Plantarum* 97: 757-763.
- Morison, J.I.L. and D.W. Lawlor. (1999). Interactions between increasing CO₂ concentration and temperature on plant growth. *Plant Cell and Environment* 22: 659-682.
- Morison, J.I.L. and R.A. Gifford. (1984). Plant growth and water use with limited water supply high CO₂ concentrations. *Australian Journal of Plant Physiology* 11: 361-374.
- Mortley, D.G., P.A. Loretan, J.H. Hill and J. Seminara. (1997). CO₂ enrichment influences yields of Florunner, Gerogia Red and New Mexico peanut cultivars. *Advances in Space Research* 20: 1905-1908.
- Murray, D.R. (1995). Plant responses to carbon dioxide. *American Journal of Botany* 82: 690-697.
- Murray, D.R. (1997). *Carbon Dioxide and Plant Responses*. Research Studies Press Ltd, Somerset, England.
- Ntare, B.R., J.H. Williams and F. Dougbedji. (2001). Evaluation of groundnut genotypes for heat tolerance under field conditions in a Sahelian environment using a simple physiological model for yield. *Journal of Agricultural Science* 136: 81-88.
- Ortega, J.L., F. Sanchez, M. Soberon and M.L. Flores. (1992). Regulation of nodule glutamine-synthetase by CO₂ levels in bean (*Phaseolus vulgaris* L.). *Plant Physiology* 98: 584-587.
- Overdieck, D., C. Reid and B.R. Strain. (1988). The effects of preindustrial and future CO₂ concentrations on growth, dry matter production and the C/N relationship in plants at low nutrient supply: *Vigna unguiculata* (Cowpea), *Abelmoschus esculentus* (Okra) and *Raphanus sativus* (Radish). *Angewandte Botanik* 62: 119-134.
- Pan, D. (1996) *Soybean Responses to Elevated Temperature and Doubled CO₂*. PhD Dissertation. University of Florida, Gainesville, USA. Dissertation Abstracts International 57, no. 10B, (1996): 5987. Accession No. AAG709292.
- Phillips, D.A., K.D. Newell, S.A. Hassell and C.E. Felling. (1976). The effect of CO₂ enrichment on root nodule development and symbiotic N₂ reduction in *Pisum sativum* L. *American Journal of Botany* 63: 356-362.
- Pickering, N.B., L.H. Allen, Jr., S.L. Albrecht, P. Jones, J.W. Jones and J.T. Baker. (1994). Environmental plant chambers: controls and measurements using CR-10T data loggers. pp. 29-35. In: D.G. Watson, F.S. Zuzueta and T.V. Harrison. (eds.).

- Computers in Agriculture: Proceedings of the 5th International Conference, Orlando, Florida 5-9 Feb.* American Society of Agricultural Engineers, St. Joseph, Michigan, USA.
- Piper, E.L. and K.J. Boote. (1999). Temperature and cultivar effects on soybean seed oil and protein concentrations. *Journal of American Oil Chemists Society* 76: 1233-1241.
- Polley, H.W. (2002). Implications of atmospheric and climate change on crop yield and water use efficiency. *Crop Science* 42: 131-140.
- Porter, M.A. and B. Grodzinski. (1984). Acclimation to high CO₂ in bean: carbonic anhydrase and ribulose biphosphate carboxylase. *Plant Physiology* 74: 413-416.
- Prasad, P.V.V., K.J. Boote, L.H. Allen, Jr. and J.M.G. Thomas. (2002). Effects of elevated temperature and carbon dioxide on seed-set and yield of kidney bean (*Phaseolus vulgaris* L.). *Global Change Biology* 8: 710-721.
- Prasad, P.V.V., P.Q. Craufurd and R.J. Summerfield. (1999). Fruit number in relation to pollen production and viability in groundnut exposed to short episodes of heat stress. *Annals of Botany* 84: 381-386.
- Prasad, P.V.V., P.Q. Craufurd and R.J. Summerfield. (2000). Effect of high air and soil temperature on dry matter production, pod yield and yield components of groundnut. *Plant and Soil* 222: 231-239.
- Prasad, P.V.V., P.Q. Craufurd and R.J. Summerfield. (2001a). Response of groundnuts dependent on symbiotic and inorganic nitrogen to high air and soil temperatures. *Journal of Plant Nutrition* 24: 623-637.
- Prasad, P.V.V., P.Q. Craufurd, R.J. Summerfield and T.R. Wheeler. (2000). Effects of short episodes of heat stress on flower production and fruit-set of groundnut (*Arachis hypogaea* L.). *Journal of Experimental Botany* 51: 777-784.
- Prasad, P.V.V., P.Q. Craufurd, V.G. Kakani, T.R. Wheeler and K.J. Boote. (2001b). Influence of high temperature during pre- and post-anthesis stages of floral development on fruit-set and pollen germination in peanut. *Australian Journal of Plant Physiology* 28: 233-240.
- Prior, S.A., H.H. Rogers, G.B. Runion and J.R. Mauney (1994). Effects of free-air enrichment on cotton root growth. *Agricultural and Forest Meteorology* 70: 69-86.
- Radoglou, K.M., P. Aphalo and P.G. Jarvis. (1992). Response of photosynthesis, stomatal conductance and water use efficiency to elevated CO₂ and nutrient supply in acclimated seedlings of *Phaseolus vulgaris* L. *Annals of Botany* 70: 257-264.
- Reardon, J.C., J.R. Lambert and B. Acock. (1990). The influence of carbon dioxide enrichment on the seasonal patterns of nitrogen fixation in soybean. In: *Responses of Vegetation to Carbon Dioxide*. Series 016, US Department of Energy and USDA-ARS, Washington DC.
- Reddy, K. R. and H.F. Hodges. (eds.) (2000). *Climate Change and Global Crop Productivity*. CABI Publishing, Oxon, UK.
- Reddy, A.R., K.R. Reddy and H.F. Hodges. (1998). Interactive effects of elevated carbon dioxide and growth temperature on photosynthesis in cotton leaves. *Plant Growth Regulation* 26: 33-40.
- Reddy, K.R., H.F. Hodges and J.M. McKinion. (1997). Crop modeling and applications: a cotton example. *Advances in Agronomy* 59: 225-290.

- Reddy, V.R., B. Acock and M.C. Acock. (1989). Seasonal carbon and nitrogen accumulation in relation to net carbon dioxide exchange in a carbon dioxide enriched soybean. *Agronomy Journal* 81: 78-83.
- Robbins, N.S. and D.M. Pharr. (1988). Effect of restricted root growth and carbohydrate metabolism and whole plant growth of *Cucumis sativus* L. *Plant Physiology* 87: 409-413.
- Rogers, H.H., C.M. Peterson, J.N. McCrimmon and J.D. Cure. (1992). Response of plant roots to elevated atmospheric carbon dioxide. *Plant Cell and Environment* 15: 749-752.
- Rogers, H.H., G.B. Runion and S.V. Krupa. (1994). Plant responses to atmospheric CO₂ enrichment with emphasis on roots and the rhizosphere. *Environmental Pollution* 83: 155-189.
- Rogers, H.H., G.B. Runion, S.V. Krupa and S.A. Prior. (1997). Plant responses to atmospheric CO₂ enrichment: implications in root-soil-microbe interactions. pp. 1-34. In: L.H. Allen, M.B. Kirkman, D.M. Olszok and C.E. Whitman (eds.). *Advances in Carbon Dioxide Effects Research*. ASA Special Publication No. 61, ASA-CSSA-SSSA, Madison, Wisconsin.
- Rogers, H.H., J.D. Cure and J.M. Smith. (1986). Soybean growth and yield response to elevated carbon dioxide. *Agricultural Ecosystems and Environment* 16: 113-128.
- Rogers, H.H., J.D. Cure, J.F. Thomas and J.M. Smith. (1984). Influence of elevated CO₂ on growth of soybean plants. *Crop Science* 24: 361-366.
- Rogers, H.H., S.A. Prior and J.M. Smith. (1986). Soybean growth and yield response to elevated carbon dioxide. *Agricultural Ecosystems and Environment* 16: 113-128.
- Sage, R.F. (1994). Acclimation of photosynthesis to increasing atmospheric CO₂—the gas exchange perspective. *Photosynthesis Research* 39: 351-368.
- Sage, R.F., T.D. Sharkey and J.R. Seemann. (1989). Acclimation of photosynthesis to elevated CO₂ in 5 C₃ species. *Plant Physiology* 89: 590-596.
- Sapra, V.T. and A.O. Anaele. (1991). Screening soybean genotypes for drought and heat tolerance. *Journal of Agronomy and Crop Science* 167: 96-102.
- Serraj, R., T.R. Sinclair and L.H. Allen, Jr. (1998). Soybean nodulation and N₂ fixation response to drought under carbon dioxide enrichment. *Plant Cell and Environment* 21: 491-500.
- Sharkey, T.D., J.A. Berry and K. Raschke. (1985). Starch and sucrose synthesis in *Phaseolus vulgaris* as affected by light, CO₂, and abscisic acid. *Plant Physiology* 77: 617-620.
- Sionit, N., B.R. Strain and E.P. Flint. (1987a). Interaction of temperature and CO₂ enrichment on soybean-growth and dry matter partitioning. *Canadian Journal of Plant Science* 67: 59-67.
- Sionit, N., B.R. Strain and E.P. Flint. (1987b). Interaction of temperature and CO₂ enrichment on soybean-photosynthesis and seed yield. *Canadian Journal of Plant Science* 67: 629-636.
- Sionit, N., H.H. Rogers, G.E. Bingham and B.R. Strain. (1984). Photosynthesis and stomatal conductance with CO₂-enrichment of container- and field-grown soybeans. *Agronomy Journal* 76: 447-451.
- Socias, F.X., H. Medrano and T.D. Sharkey. (1993). Feedback limitation of photosynthesis of *Phaseolus vulgaris* L. grown in elevated CO₂. *Plant Cell and Environment* 16: 81-86.

- Srinivasan, A., H. Takeda and T. Senboku. (1996). Heat tolerance in food legumes as evaluated by cell membrane thermostability and chlorophyll fluorescence techniques. *Euphytica* 88: 35-45.
- Stancel, K., D.G. Mortley, D.R. Hileman, P.A. Loretan, C.K. Bonsi and W.A. Hill. (2000). Growth, pod, and seed yield, and gas exchange of hydroponically grown peanut in response to CO₂ enrichment. *Hortscience* 35: 49-52.
- Stitt, M. (1991). Rising CO₂ levels and their potential significance for carbon flow in photosynthetic cells. *Plant Cell and Environment* 14: 741-762.
- Stronach, I.M., S.C. Clifford, A.D. Mohamed, P.R. Singletonjones, S.N. Azamali and N.M.J. Crout. (1994). The effects of elevated carbon dioxide, temperature and soil moisture on the water-use of stands of groundnut (*Arachis hypogaea* L.). *Journal of Experimental Botany* 45: 1633-1638.
- Tardieu, F. and W.J. Davis. (1993). Integration of hydraulic and chemical signaling in the control of stomatal conductance and water status of droughted plants. *Plant Cell and Environment* 16: 341-349.
- Thomas, J.F. and C.N. Harvey. (1983). Leaf anatomy of four species grown under continuous CO₂ enrichment. *Botanical Gazette* 144: 303-309.
- Thomas, J.M.G. (2001). *Impact of Elevated Temperature and Carbon Dioxide on Development and Composition of Soybean Seed*. PhD Dissertation. University of Florida, Gainesville, USA. Dissertation Abstracts International 62, no. 09B, (2001): 3856. Accession No. AAI3025125.
- Thomas, J.M.G., K.J. Boote, L.H. Allen, Jr., M. Gallo-Meagher and J.M. Davis. (2003). Elevated temperature and carbon dioxide effects of soybean seed composition and transcript abundance. *Crop Science* 43:1548-1557.
- Thomas, R.B. and K.L. Griffin. (1994). Direct and indirect effects of atmospheric carbon dioxide enrichment on leaf respiration of *Glycine max* (L.) Merr. *Plant Physiology* 104: 355-361.
- Valle, R., J.W. Mishoe, J.W. Jones and L.H. Allen, Jr. (1985b). Transpiration rate and water-use efficiency of soybean leaves adapted to different CO₂ environments. *Crop Science* 25: 477-482.
- Valle, R., J.W. Mishoe, W.J. Campbell, J.W. Jones and L.H. Allen, Jr. (1985a). Photosynthetic responses of Bragg soybean leaves adapted to different CO₂ environments. *Crop Science* 25: 333-339.
- Vu, J.C.V., L.H. Allen, Jr. and G. Bowes. (1989). Leaf ultra-structure, carbohydrates, and protein of soybeans grown under CO₂ enrichment. *Environmental and Experimental Botany* 29: 141-147.
- Vu, J.C.V., L.H. Allen, Jr., K.J. Boote and G. Bowes. (1997). Effects of elevated CO₂ and temperature on photosynthesis and Rubisco in rice and soybean. *Plant Cell and Environment* 20: 68-76.
- Vu, J.C.V., R.W. Gesch, A.H. Pennanen, L.H. Allen, Jr., K.J. Boote and G. Bowes. (2001). Soybean photosynthesis, Rubisco and carbohydrate enzymes function at supra-optimal temperatures in elevated CO₂. *Journal of Plant Physiology* 158: 295-307.
- Wheeler, T.R., A. Chatzialioglou, P.Q. Craufurd, R.H. Ellis and R.J. Summerfield. (1997). Dry matter partitioning in groundnut exposed to high temperature stress. *Crop Science* 37: 1507-1513.

- Wheeler, T.R., P.Q. Craufurd, R.H. Ellis, J.R. Porter and P.V.V. Prasad. (2000). Temperature variability and the yield of annual crops. *Agriculture Ecosystems and Environment* 82: 159-167.
- Williams, L.E., T.M. DeJong and D.A. Phillips. (1981). Carbon and nitrogen limitations on soybean seedling development. *Plant Physiology* 68: 1206-1209.
- Wolf, R.B., J.F. Cavins, R. Kleiman and L.T. Black. (1982). Effect of temperature on soybean seed constituents-oil, protein, moisture, fatty acids, amino acids and sugars. *Journal of the American Oil Chemists Society* 59: 230-232.
- Wu, W.H., J.Y. Lu, D.G. Mortley, P.A. Loretan, C.K. Bonsi and W.A. Hill. (1997). Proximate composition, amino acid profile, fatty acid composition, and mineral content of peanut seeds hydroponically grown at elevated CO₂ levels. *Journal of Agricultural and Food Chemistry* 45: 3863-3866.
- Zhang, J. and W.J. Davis. (1987). Increased synthesis of ABA in partially dehydrated root tips and ABA transport from roots to leaves. *Journal of Experimental Botany* 38: 2015-2023.
- Ziska, L.H., J.A. Bunce and F.A. Caulfield. (2001). Rising atmospheric carbon dioxide and seed yield of soybean genotypes. *Crop Science* 41: 385-391.